The following papers were read :—

1 Contributions to the Morphology of the Group Neritacea of Aspidobranch Gastropods.—Part I. The *Neritidæ*. By Prof. Gilbert C. Bourne, D.Sc., F.Z.S.

[Received October 27, 1908.]

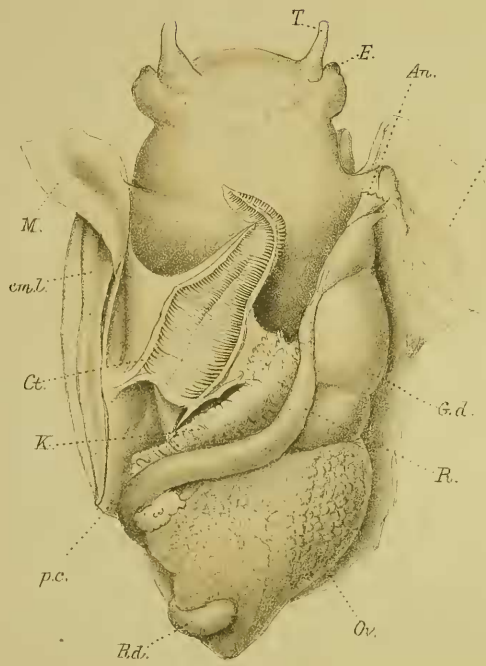
(Plates XLVI.–LXVI.* and Text-figure 172.)

While the Haliotidæ, Fissurellidæ, Pleurotomariidæ, Trochidæ, Patellidæ, and other members of the Aspidobranch Gastropoda have received a large amount of attention from morphologists, the Neritacea have, until recent years, attracted little interest. The anatomy of so familiar a species as the European *Neritina fluviatilis* was imperfectly known till the appearance of Lenssen's memoirs in 1899 (**25**) and 1903 (**26**). Thiele's (**39**) short but accurate descriptions of various organs of tropical species of Neritidæ have added largely to our knowledge of the group, but even when these are taken into consideration it can hardly be said that a sufficiently comprehensive comparative account of the Neritidæ exists in a form available for students of molluscan anatomy.

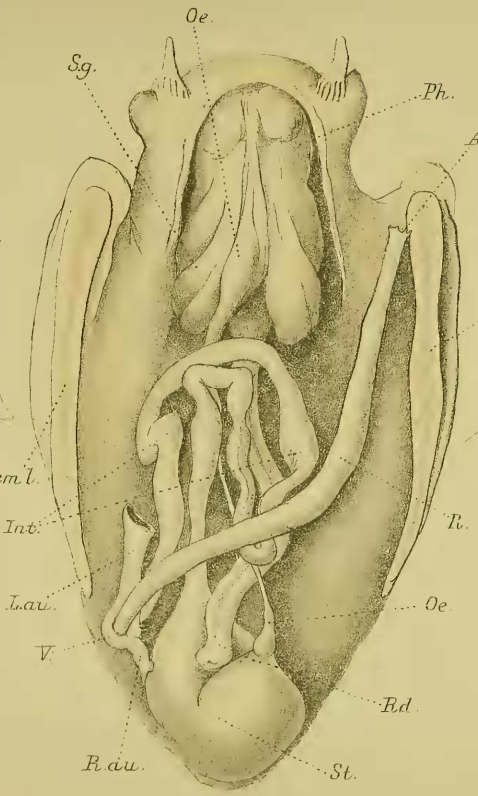
It has been too readily assumed that the Neritacea, forming, as they do, an extremely specialized section of the Rhipidoglossa, are unlikely to retain any considerable traces of primitive organization, or to yield evidence bearing on the ancestry of the Gastropoda. Thus Pelseneer (**30**) writes: "D'autre part les Néritacés sont plus spécialisés que tous les autres Rhipidoglosses (*Haliotis* etc.) ou la commissure viscérale est déjà croisée, par: 1°. L'existence d'une seule branchie et d'un seul osphradium. 2°. L'existence d'un seul rein. 3°. L'existence d'un orifice genital propre. 4°. L'existence d'yeux à cavité fermée. 5°. La séparation plus complète des ganglions pleuraux et pedieux." There is no doubt that the Neritacea are specialized in these respects, but this is no reason for regarding them as probably uninteresting subjects for anatomical study, for animals highly specialized in some respects may, nevertheless, retain many primitive features, and there are so many points in which the Neritacea seem to approximate to the Pectinibranchs, *e. g.* the existence of a single kidney with a slit-shaped opening into the mantle-cavity, the complex genital ducts with accessory glands, &c., that it has long been a matter of interest to determine whether they are intermediate between the less specialized Aspidobranchia and the Pectinibranchia, or whether their apparent resemblances to the latter group are due to convergence.

Finally, the Helicinidæ, interesting because they are terrestrial and pulmonate, have not been the subject of any comprehensive

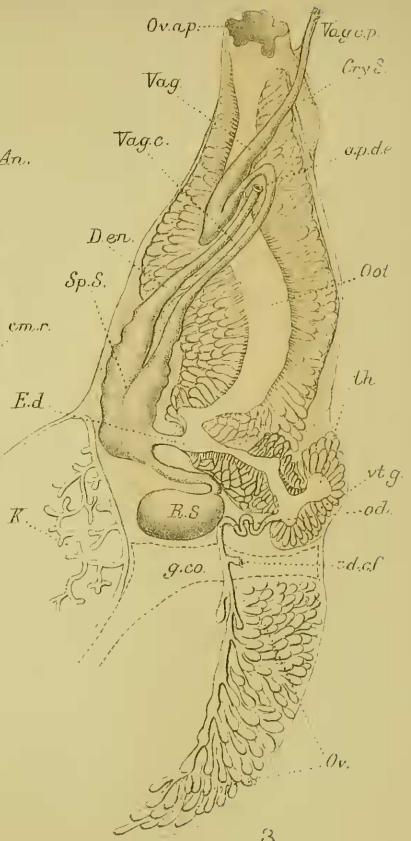
* For explanation of the Plates see p. 884.



1.



2.

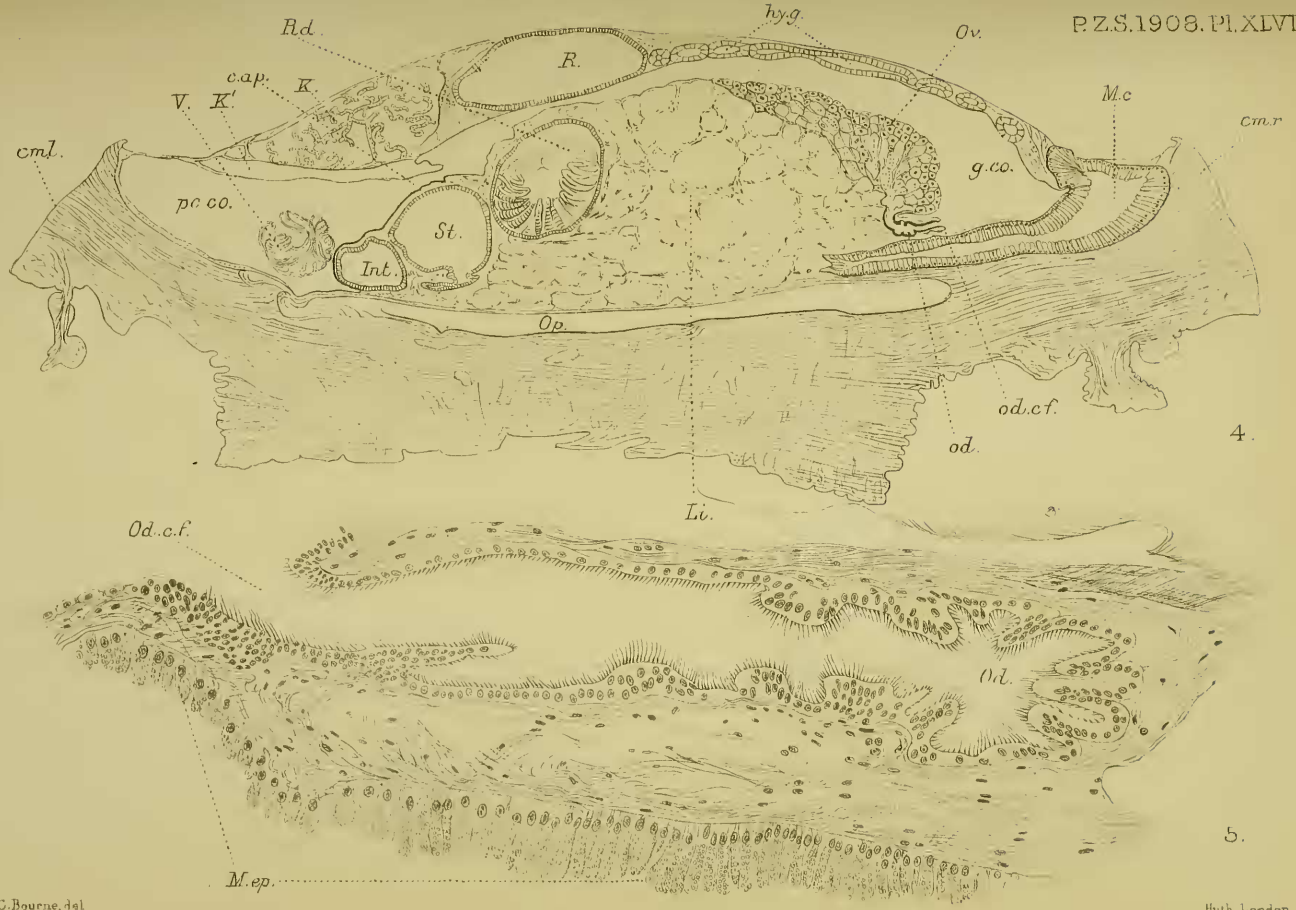


3.

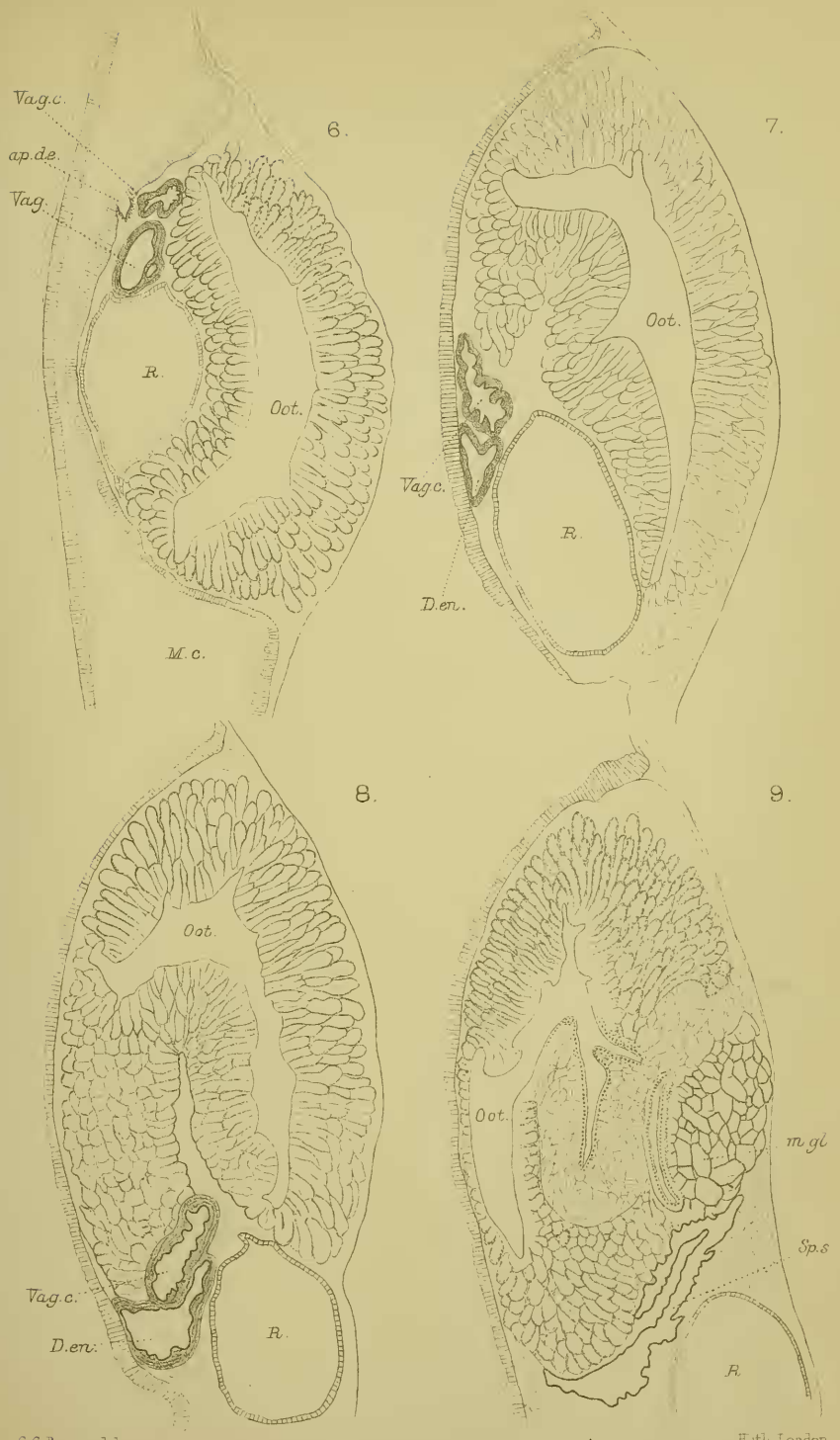
G.C. Bourne del

Ruth London.

SEPTARIA BORBONICA

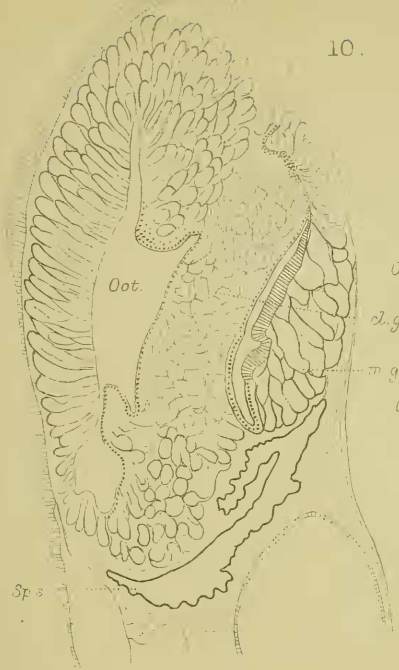


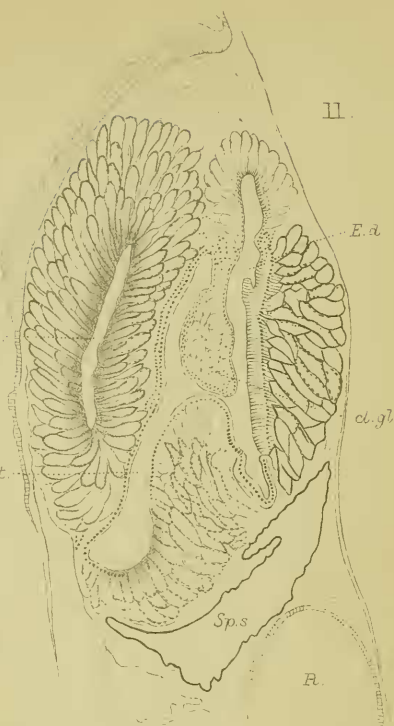
CŒLOM & OVIDUCO-CŒLOMIC FUNNEL OF SEPTARIA.

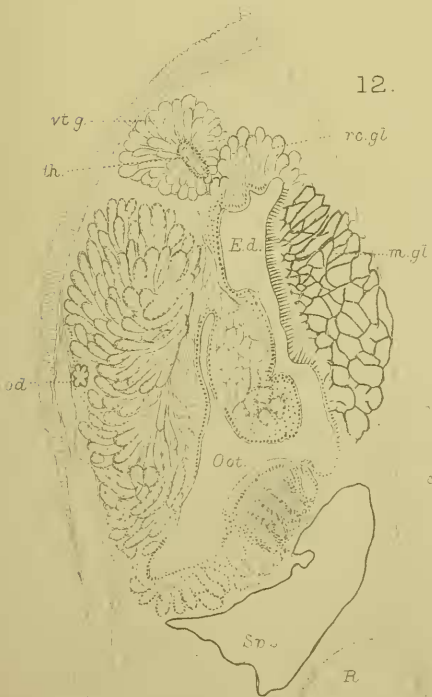


G.C.Bourne del. Hutt. London.

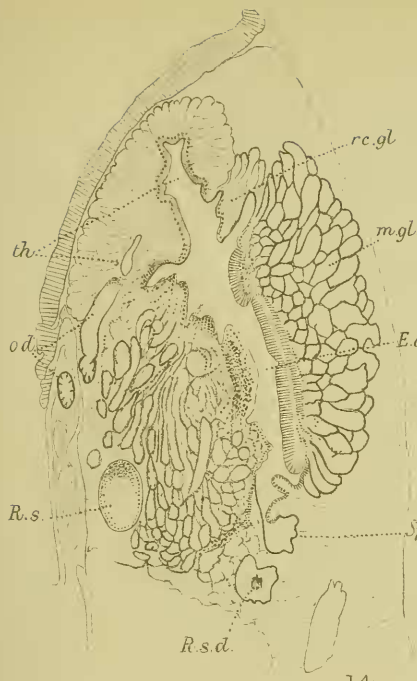
GENITAL COMPLEX OF SEPTARIA BOUGAINVILLEI ♀



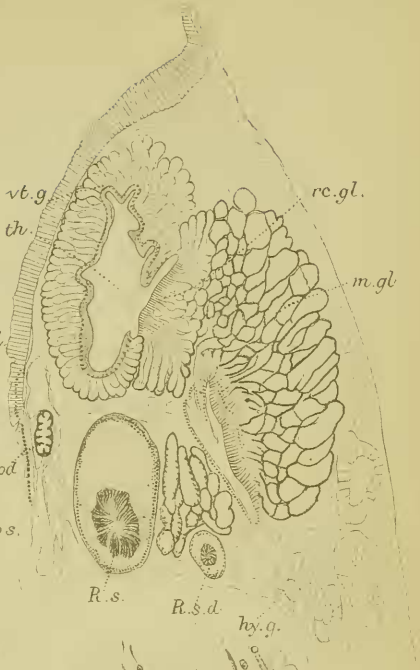




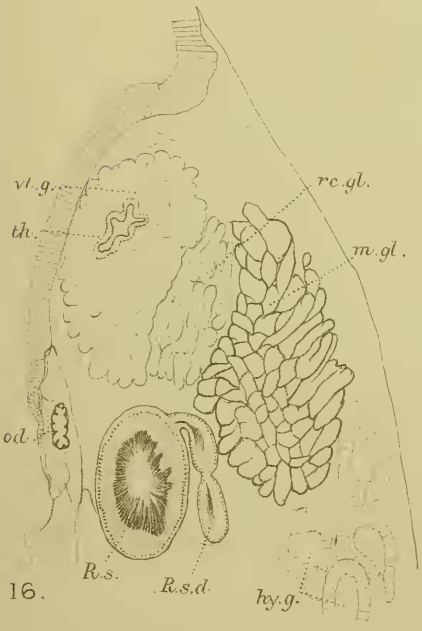
GENITAL COMPLEX OF SEPTARIA BOUGAINVILLEI ♀.



14.



15.



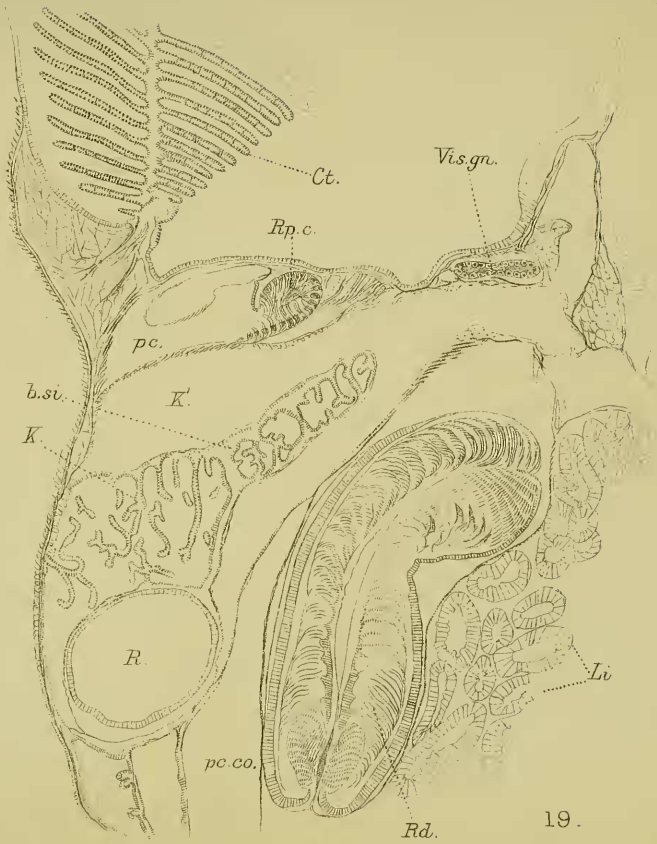
16.

17.

G.C.Bourne del. Huth. London.

FEMALE DUCTS & OSPHRADIUM OF SEPTARIA.

18.

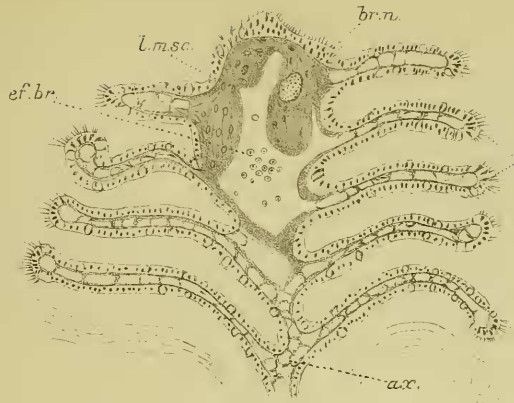


19.

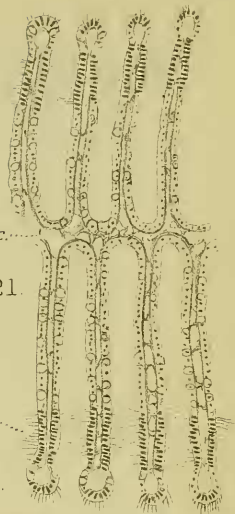
G C. Bourne del.

Huth, London.

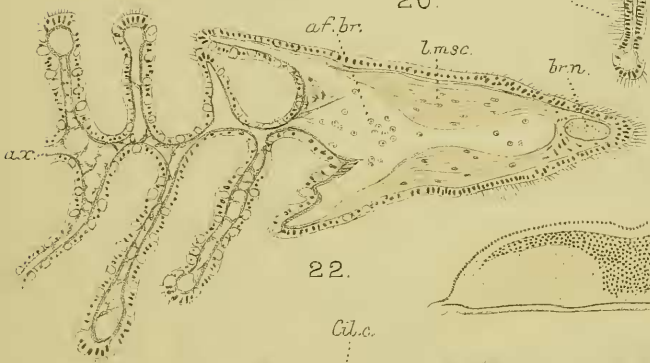
KIDNEY OF SEPTARIA DEPRESSA.



20.

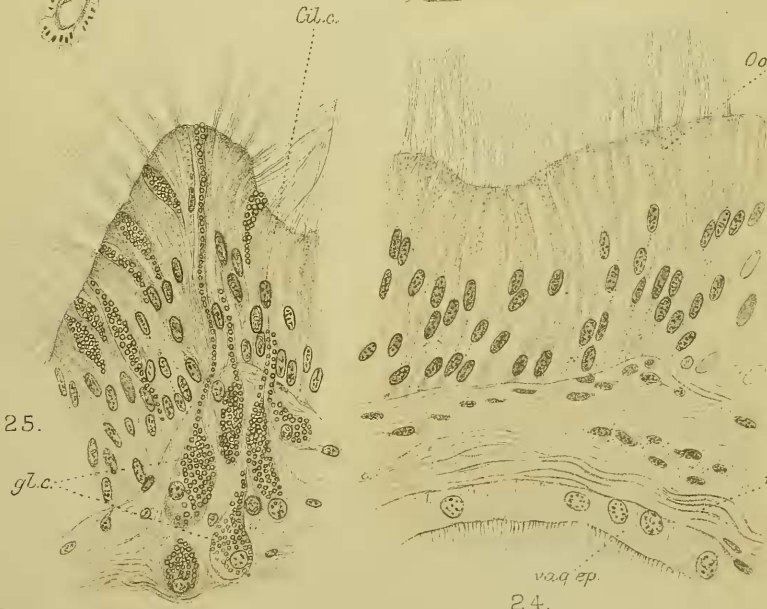


21.



22.

23.

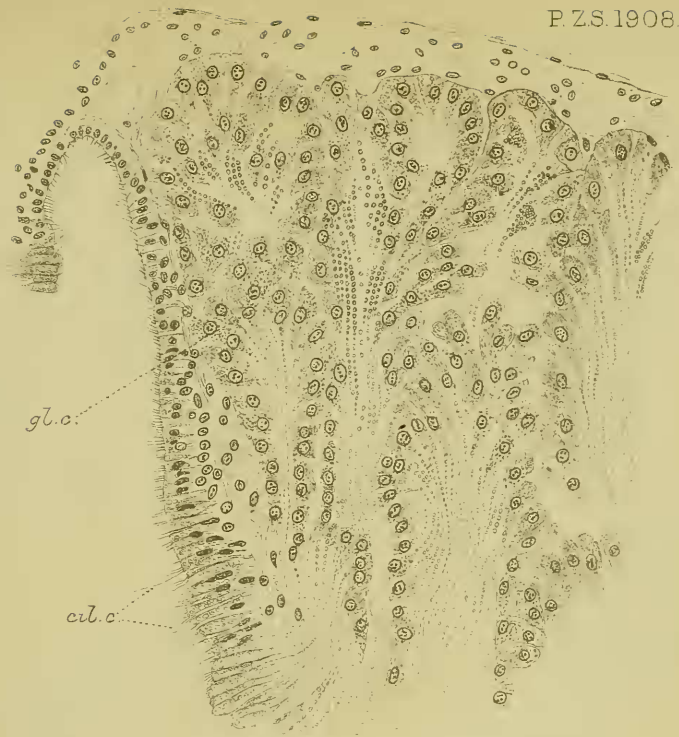


25.

24.

G. C. Bourne del. Hutn. London

GILL-LAMELLÆ ETC. OF SEPTARIA.



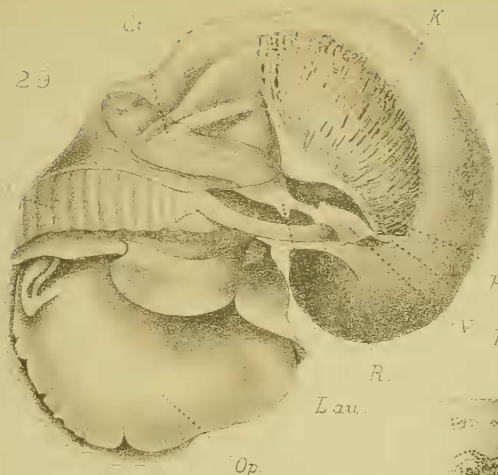
26.

27.

28.

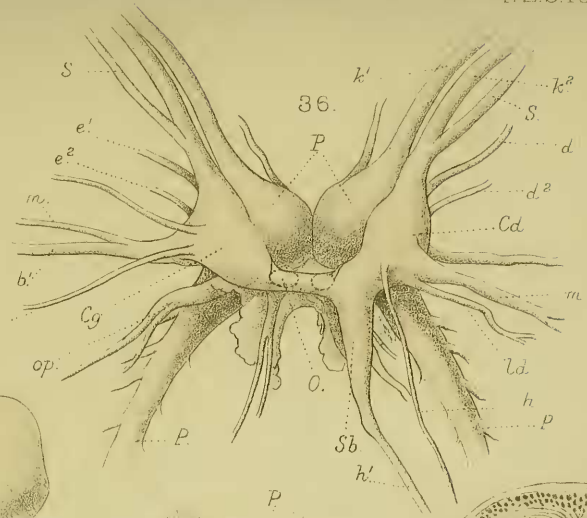
G. C. Bourne del.
Huth, London.

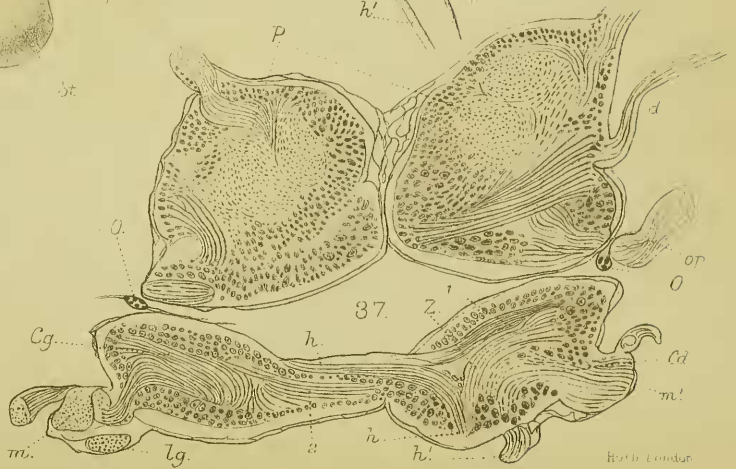
HISTOLOGY OF GENITAL DUCTS OF SEPTARIA.



ANATOMY OF NERITA, PARANERITA & NERITINA.

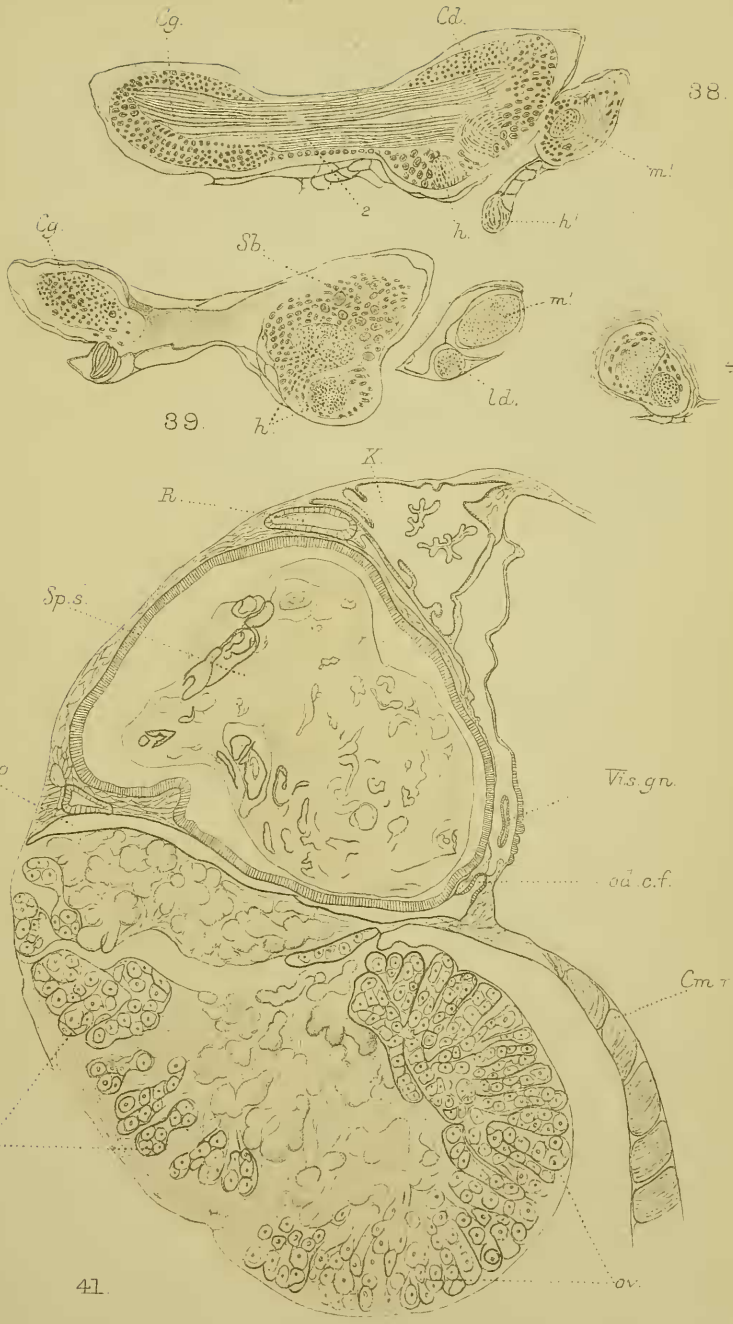
35.





G.C. Bourne del.

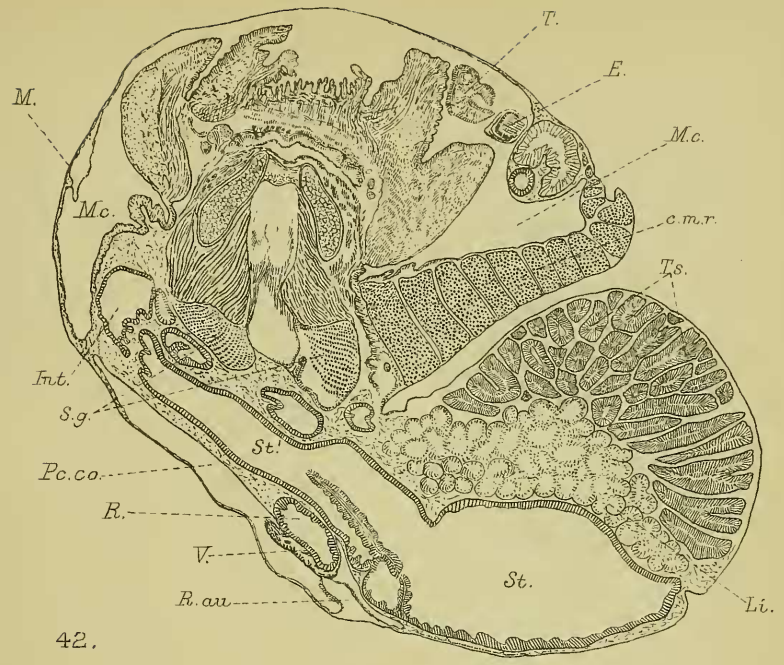
ALIMENTARY TRACT & NERVOUS SYSTEM OF PARANERITA.



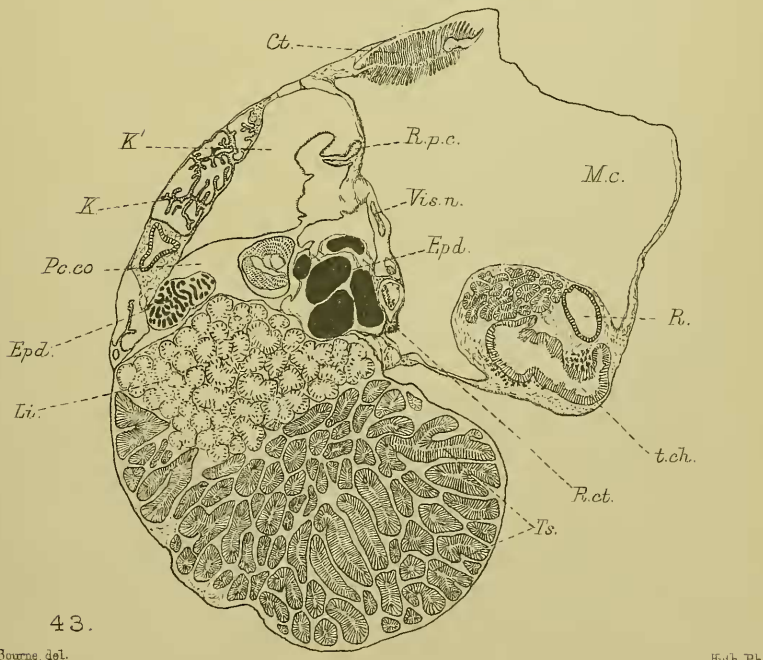
G. C. Bourne del.

Huth London.

ANATOMY & HISTOLOGY OF NERITIDAE.



42.

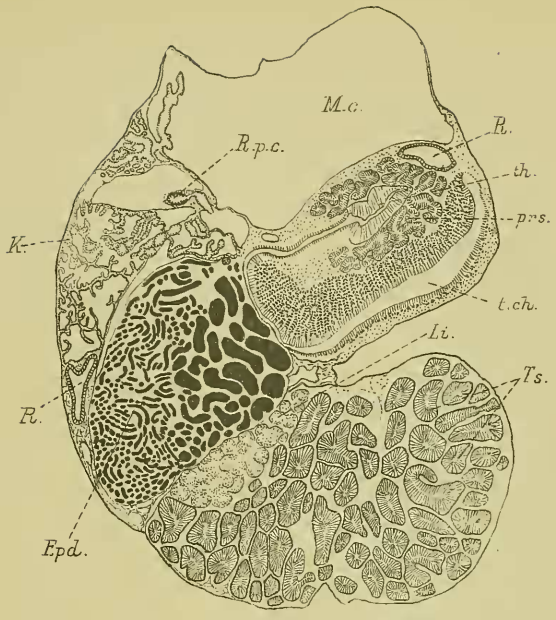


43.

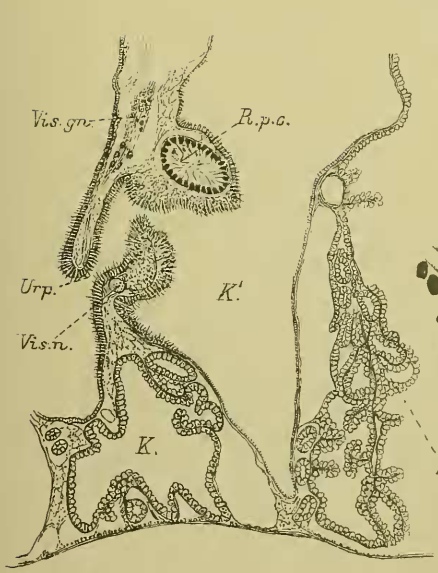
G.C. Bourne, del.

Hulh, Phot.

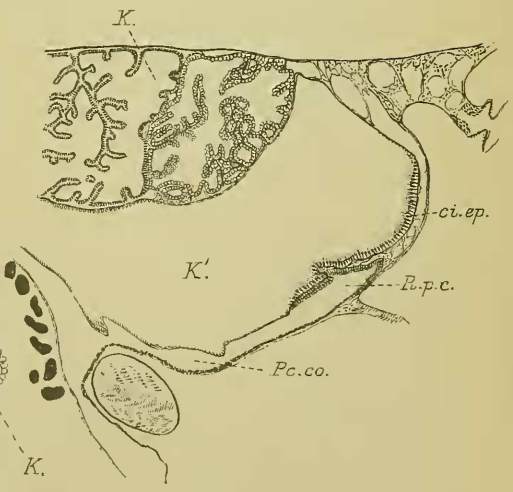
PARANERITA GAGATES.



44.



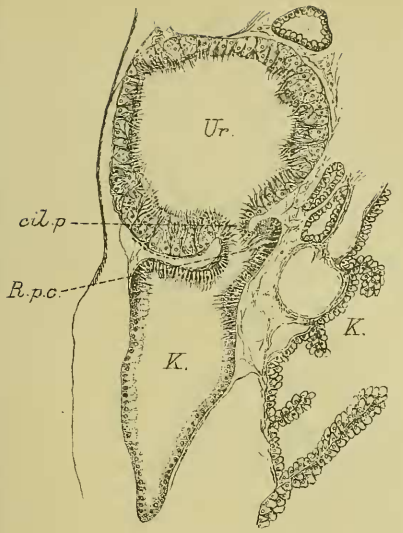
45.



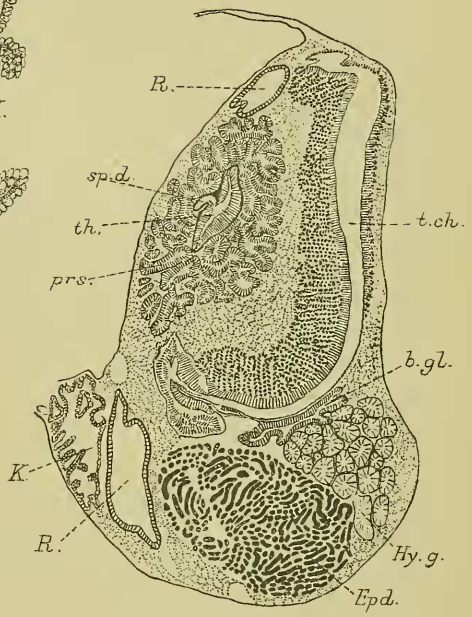
46.

G.C. Bourne, del. Huth Phot.

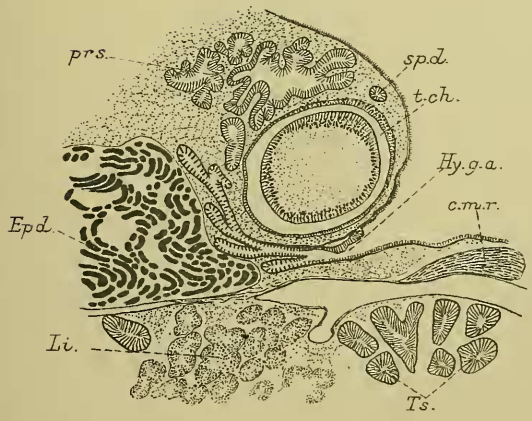
PARANERITA VARIEGATA AND GAGATES.


Ur.
cil.p
R.p.c
K.
K.

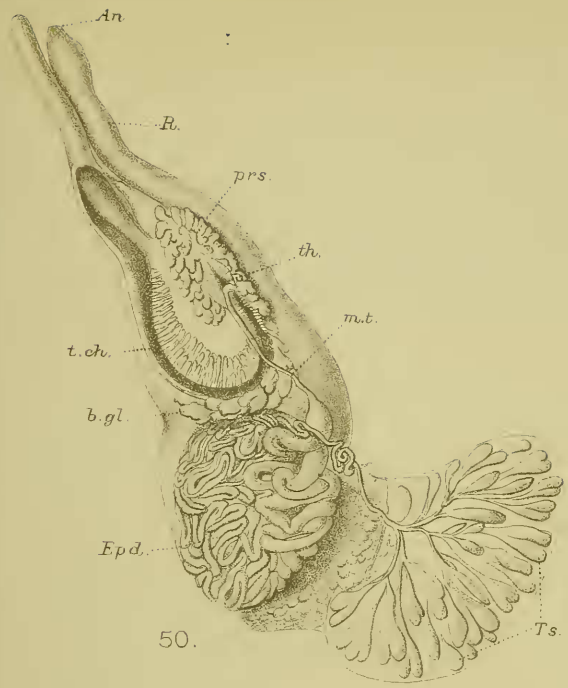
47.


R.
sp.d.
th.
t.ch.
prs.
b.gl.
K.
R.
Hy.g.
Epd.

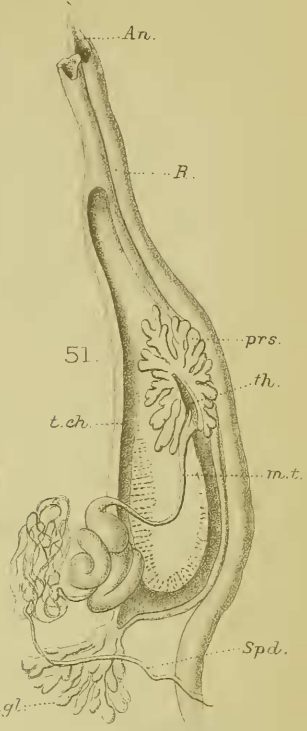
48.


prs.
sp.d.
t.ch.
Hy.g.a.
c.m.r.
Epd.
Li.
Ts.

49.



50.

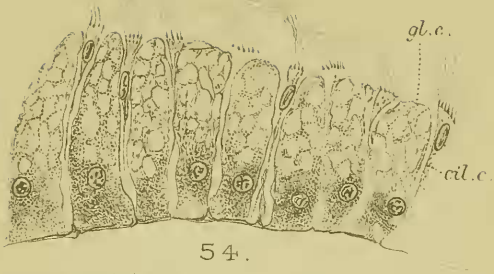


51.

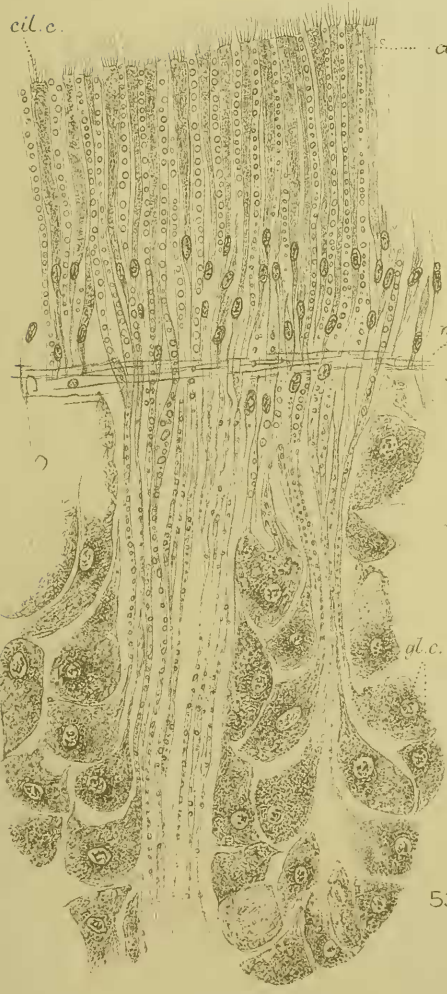
52.

G.C.Bourne del. Huth, London.

MALE DUCTS OF NERITA AND PARANERITA.



54.



53.

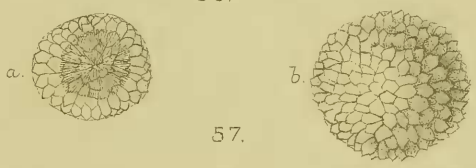
55.

C.C.Bourne del

Erth London

MALE DUCTS OF PARANERITA.

56.



57.

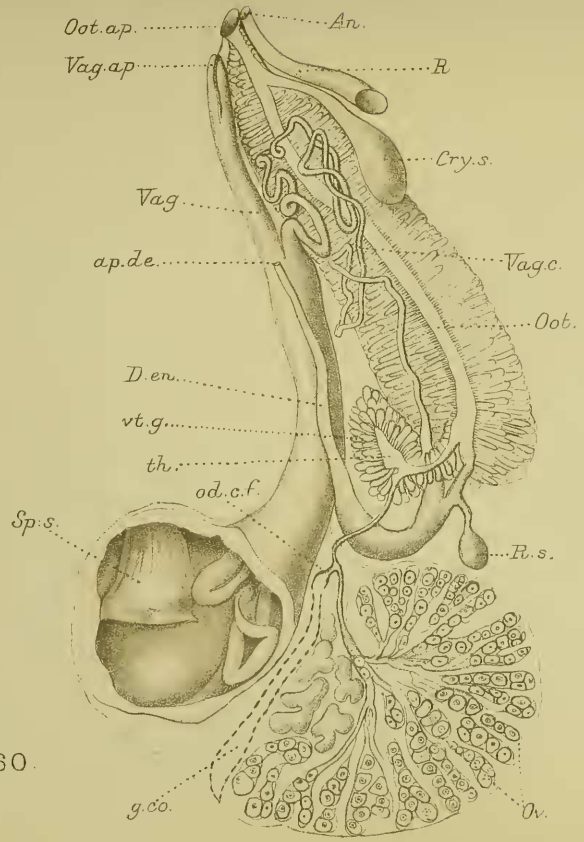
58.

59.

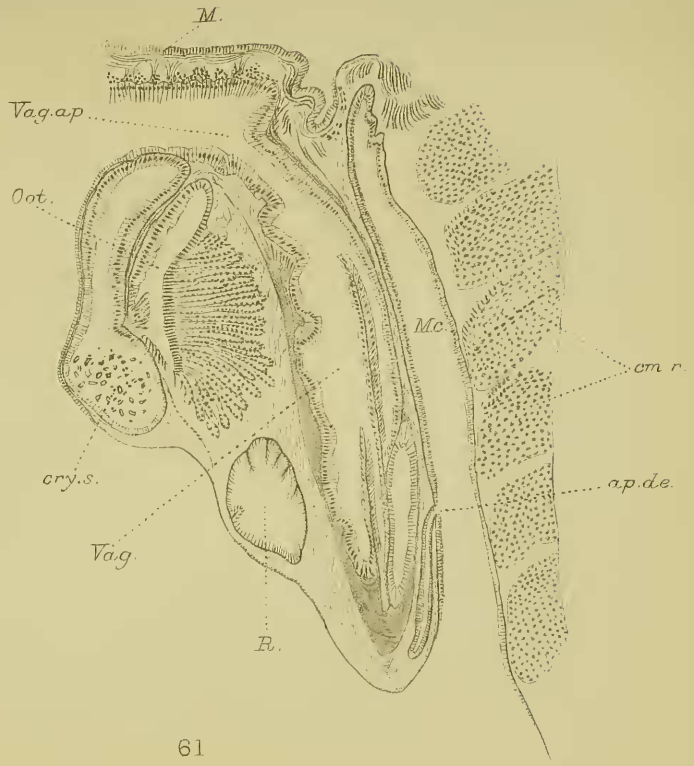
G.C. Bourne, del.

Huth, London

ANATOMY & HISTOLOGY OF NERITIDAE



60.



61

G.C. Bourne del

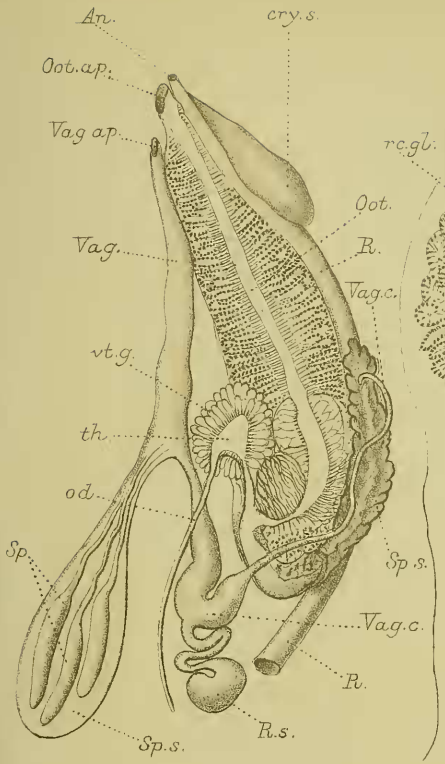
Huth, London

REPRODUCTIVE ORGANS OF PARANERITA ♀.

G C Bourne del

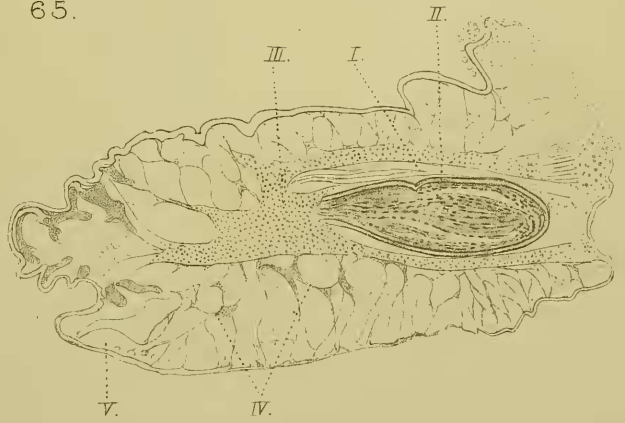
Huth, London

FEMALE ORGANS OF PARANERITA.



65.

67.

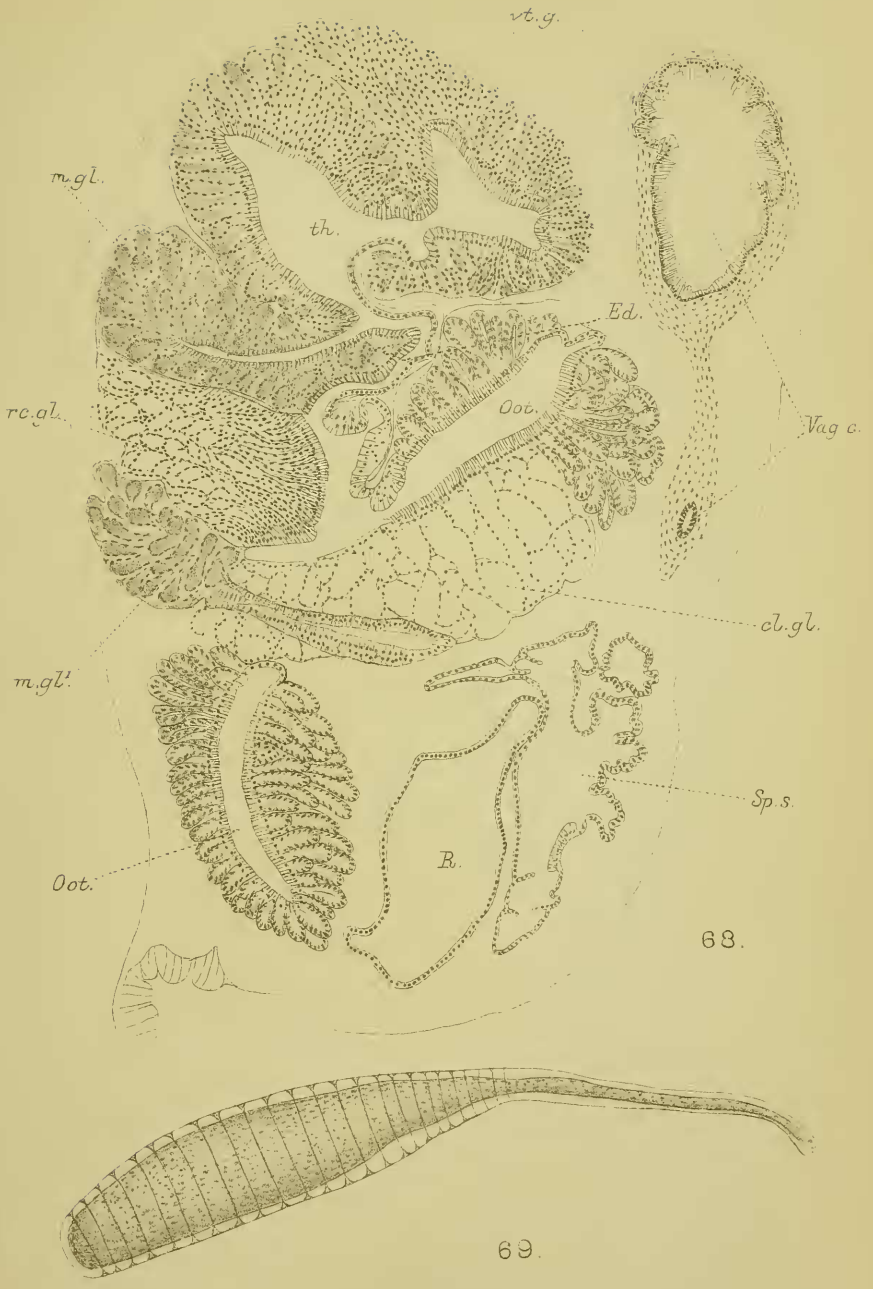


66.

G.C. Bourne, del.

Huth, London.

REPRODUCTIVE ORGANS OF NERITA PLICATA ♀.



G.C. Bourne del. Huth, London.

REPRODUCTIVE ORGANS OF NERITA PLICATA ♀.

anatomical memoir since Isenkrahe published an incomplete account of their structure in 1867, and it is high time that this gap in our knowledge of Gastropodan anatomy should be filled up. If comparative anatomists have given but small heed to the Neritacea, the conchologists and systematists have done their full share of work on the group, and the works of Martens (**27**) and Pilsbry and Tryon (**40**) give a most complete account from a taxonomical point of view. But, as is often the case when classification is founded on external characters only, such as the shell and the operculum, a more complete study shows that it rests on insecure foundations; and while I am unable to do more than criticize the genera *Nerita* and *Neritina* as usually defined, I shall bring forward evidence which will, I hope, induce authors more conveniently situated for the study of these forms than I am to undertake a revision of the family Neritidæ, based upon anatomical characters.

The name Neritacea—the group has not been raised to the rank of a suborder or even of a tribe or section—was used by Lamarck as a collective designation for the recent families of Neritidæ, Neritinidæ, and Helicinidæ. To these have been added the Neritopsidæ, Titiscaniidæ, Scutellinidæ, Hydrocenidæ, and Proserpinidæ, and the fossil families Maclureidæ and Naticopsidæ.

It is not part of my present intention to criticize the recent and extinct families and genera that have been founded by conchologists, nor to discuss the probable relationships of the palæozoic forms which, like the genus *Deshayesia*, have been held to occupy a position intermediate between the Neritidæ and Naticidæ (see Pethö (**33**), who refers it to the latter family). But as it will appear in the latter part of this paper that the result of my anatomical investigations is to show that the Neritacea retain some primitive characters, and in so far as they are specialized do not show any approximation to the Pectinibranchia, but are contrariwise modified in a special direction, which culminates in the terrestrial Helicinidæ, &c., it is of interest to consider how far the group may be regarded as of undoubted geological antiquity. The family Neritidæ is of respectable antiquity. The genus *Nerita* is represented by the subgenus *Lissochilus* Pethö in the Triassic and Jurassic, and by the subgenus *Otostoma* d'Archiac in the Cretaceous of Europe, Algiers, and Asia Minor. The genus *Deshayesia*, which is considered by some conchologists to "present a very remarkable combination of the characters of *Nerita* and *Natica* and appears to establish a passage between those genera" (Pilsbry and Tryon, vol. x. p. 5), is from the Eocene and Miocene of the Paris and Bordeaux basins, and if it is really a Neritid, its Naticid characters must be due to convergence and must not be taken as indicating a passage between the Aspidobranchiate and Pectinibranchiate Gastropods, for such a passage must have been effected long before the Tertiary period.

The genus *Neritina*, if indeed it is as distinct from *Nerita* as

conchologists assume, is found fossil from the Liassic onward, and is most numerous in species in the Miocene and Pliocene. The subgenus *Neritodonta* Brusina, from the Tertiary of Dalmatia, is of special interest, as being possibly a forerunner of the pulmonate *Hydrocena*, now living in the same region. The genus *Neritoma* Morris is found in the Jurassic of Europe, and the subgenera *Neridomus* Morris and Lycett and *Onchochilus* Pethö in the Oolite and the Triassic and Jurassic respectively. The genus *Deianira* Stoliczka is from the lacustrine deposits of the Cretaceous of Europe, and *Velates* Montfort from the Tertiaries of Europe, India, and Madagascar. The limpet-like *Pileolus* Sowerby, resembling the modern *Septaria*, dates from the Jurassic and Cretaceous. The Neritopsidæ, differing from the Neritidæ in the characters of radula and operculum, are represented by a single recent species, *Neritopsis radula*, from the E. Indies and Polynesia, but are fossil from the Secondaries and Tertiaries. Since, with the exception of *Deshayesia*, there is no doubt as to the relationship of these extinct genera, it is clear that even in earlier Secondary times the Neritacea were differentiated into marine, estuarine, and freshwater forms more or less resembling those of the present day, and must have been derived from an earlier stock, which we may look for in primary formations. But the remains of Neritacea from palæozoic deposits are at the best doubtful. As for some species of *Nerita* which have been described from this period, it is only necessary to quote von Martens (27): "Einige angebliche Arten von Nerita aus den palæozoischen Formationen sind betreffs der Gattung höchst zweifelhaft, wie es überhaupt meist eine unsichere und hoffnungslose Sache ist, palæozoische Gastropoden auf Gattungen der Gegenwart zu beziehen."

The family Maclureidæ, of which *Maclurea* Lesueur, from the Cambrian and Silurian of N. America and Scotland, is the sole genus, is placed near the Neritidæ because of its opercular apophyses, but its affinities are very doubtful, and it has at various times been placed in the Solariidæ, Atlantidæ, Pleurotomariidæ, or between the Bellerophontidæ and Haliotidæ. *Naticopsis* M'Coy, ranging from the Devonian to the Trias, and the subgenus *Trachydomia* Meek and Worthen, from the Carboniferous, are placed in the Neritopsidæ because of the characters of the operculum, but the shell is more like that of the Naticidæ. If these palæozoic genera are really allied to the Neritacea, the latter group is of great antiquity. On the other hand, the most specialized of all the Neritacea, the pulmonate Helicinidæ, Hydrocenidæ, and Proserpinidæ, are only found in late tertiary deposits, and have clearly been evolved in comparatively recent time from Neritiform ancestors.

The sole exception to this statement is furnished by the genus *Dawsoniella* from the Carboniferous of Illinois. It is found in association with shells of the genus *Pupa*, and there can be no doubt that it was of terrestrial habit. Formerly placed in the

genus *Helix*, it is now regarded as a member of the Helicinidæ, but differs from the latter in possessing a large basal columellar callosity covering the umbilical region. The operculum is apparently unknown. The affinities of *Dawsoniella* must be considered doubtful, but in any case its resemblance to the Helicinidæ is to be regarded as due to convergence, and not to natural affinity. In the first place, it is highly improbable that if Helicinidæ had existed from the Carboniferous onwards, no trace of their remains should have been discovered in secondary and earlier tertiary deposits. In the second place, the Helicinidæ are unquestionably derived from the Neritidæ, and, as we have seen, the Neritidæ were not established in Carboniferous times. It is interesting, however, to note that the genus *Naticopsis* (*Trachydomia*) occurs in the same formation as *Dawsoniella*, and it seems probable that we have here an interesting case of parallel development. If *Naticopsis*, a marine form, was the forerunner of the later Neritidæ, it would seem to have given rise in Carboniferous times to the terrestrial *Dawsoniella*, just as the marine Neritidæ have given rise in later time to the terrestrial Helicinidæ; and the ancestry and conditions of life being similar, the two terrestrial forms acquired such a similitude that their shells have been classified together in the same family.

Though the several genera of recent Neritacea have been studied with minute care from a systematic point of view, we have no very satisfying account of their habits. The genus *Nerita* is confined to tropical or subtropical seas, and if we accept for the moment the limitations of the genus as defined by conchologists, all the species are marine and are found for the most part between tide-marks, clinging like limpets to the rocks. Some of the more brightly coloured species live on coral-banks. It has been remarked by several travellers that they are capable of enduring a considerable amount of exposure to the air. Thus Quoy and Gaimard (**36**) were surprised to see *Neritæ* attached to black rocks under the full glare of a tropical sun, without apparent injury, and they observed that these animals always retained a few drops of water in their shells which they ejected when forcibly torn from their attachment. C. B. Adams observed a West-Indian species living in crevices in the rocks between the tide-marks at the height of three-quarter ebb-tide, and the young forms were even higher up, attached to rocks and stones which were only wetted by spray. Practically nothing is known of the breeding-habits of *Nerita*, and in view of the complexity of the accessory genital organs, especially in the female, observations on this point are very much to be desired.

As to the extent to which different species of *Nerita* are tolerant of brackish or even of fresh water, very little information of a satisfactory character is forthcoming. Many species are recorded from bays at the mouths of rivers or from estuaries, where there must be a considerable admixture of fresh and salt water. *Nerita lineata* Chemnitz is recorded as ascending the

Saigon River in Cochin China, as far as 20 or 25 miles from its mouth, and must therefore be capable of living in fresh or at least slightly brackish water. This species is a typical member of the genus *Nerita*, having a thick shell with spiral costæ, a denticulate outer lip, and a granular operculum, and is remarkable as being one of the few species with these characters which is tolerant of both salt and fresh water, though there are several species of *Neritina*, usually a freshwater genus, which live in brackish water or are even marine. It seems probable, however, that several species of *Nerita* are capable of existing in brackish water, since many of them are recorded from bays at the mouths of large rivers, and an observation made by Mrs. Longstaff—to whom I am indebted for some well-preserved specimens of *Nerita plicata* Linn.—shows that fresh water is not fatal even to exclusively marine species. Mrs. Longstaff attempted to kill some individuals of this species by immersing them in fresh water: they were apparently uninjured, but did not like the new conditions and crawled up the side of the vessel in which they were placed, fixing themselves round its rim, apparently ready to withstand a considerable sojourn in the air.

This question of habitat, in fresh, brackish, or salt water, is of some importance in considering the generic distinction between *Nerita* and *Neritina*. The species of the latter genus are mostly inhabitants of fresh water, and some are found only at the sources of streams, far away from the sea. The numerous European species, of which *N. fluviatilis* is the most familiar example, are freshwater forms, but occasionally occur in brackish or even salt water. Yet many of the tropical species are partly or wholly marine, e. g. *N. ualuensis* Lesson of the Indian Ocean and Polynesia. Quoy and Gaimard (**35**) found *N. auriculata* Lam. in the sea. Dr. Ed. von Martens (**27**) describes the following S. American forms as "species submarinæ." *N. virginea* is common in brackish water, but var. *listeri*, of E. Nicaragua, is found throughout the river San Juan, and also in Greytown harbour in localities where the water is alternately brackish and fresh. *N. picta* Sowerby from S. Panama was observed in abundance on a mudbank covered at times with fresh water, and has been described as strictly marine by C. B. Adams. *N. viridis*, not rare in the Mediterranean and in the Caribbean Sea, also in the Bermudas, is truly marine and lives on Zostera. From all of which it follows that whereas *Nerita* is very rarely found in fresh water, *Neritina* is much more easily accommodated to different conditions of life.

In what precedes, I have accepted the usual distinctions between the two genera founded upon the characters of shell and operculum, but it is a question, as will be more clearly shown in the sequel, whether these characters are of sufficient importance to afford generic distinctions between forms, the internal anatomy of which is, in nearly all respects, so similar as to be practically indistinguishable; and the further question will be raised as to

whether anatomical differences of an important character do not indicate the distinction of *Neritina fluviatilis*—and possibly of other nearly allied European species from the tropical forms usually classed in the same genus. It may be pointed out here that the conchological characters relied upon in the determination of the two genera are confessedly somewhat obscure. In general, *Nerita* has a thicker and more solid shell, usually ornamented with spiral ribs, but these may be absent, as in *polita*, *morio*, *picea*, &c.; when ribs are present they usually project slightly beyond the outer lip, which is then dentate, but it may be smooth. The inner surface of the outer lip is generally dentate, but this character may be absent. The operculum is usually solid, with a granular outer surface, or with a marginal zone, and the shape of the apophyses springing from its inner side is claimed to be characteristic.

Dr. Ed. von Martens (**27**), the leading authority on the classification of the Neritacea, maintains that the denticulation on the inner side of the outer lip and the characteristic sculpture of the operculum are the most constant differences between *Nerita* and *Neritina*, "in den meisten Fällen auch der allgemeine die Meerbewohnerin verkündende Habitus, der aber bei den kleineren schwarzen Arten weniger hervortritt." In *Neritina* the shell is usually thinner and less solid, not ornamented with spiral ribs, though these are present in *N. cornea* Linn. and especially in its variety *subsulcata*, and spirally arranged rows of spines or nodules are not uncommon. The outer lip is smooth and not dentate (it is distinctly crenulate in *N. granosa* Sowerb. and *N. aculeata* Gmelin) and the inner denticulations of the outer lip are wanting. The operculum is not granular or sculptured, but minute granulations may be discerned with the aid of a lens in several species; I found them specially well marked in a specimen of *N. recluziana* Guillou. As for the apophyses, after making a careful comparison of these structures in all the species of both genera that I possess, I have concluded that they offer so many examples of convergence that they are quite unreliable for the purpose of generic distinction, but, as I make no pretension to skill as a systematist, my judgment in this matter must be taken for what it is worth.

A certain number of Neritinæ have the last whorl of the shell broadly expanded, the aperture enlarged, and the spire reduced, so that they acquire a secondary symmetry; such, for instance, are *N. dilatata* Brod. and *N. crepidularia* Lam. It is interesting to note that those forms which tend towards a bilateral symmetry, such as the two species quoted, and also *N. auriculata* Lam., *N. tahitensis* Lesson, *N. bicanaliculata* Récluz, are all from the Indian or Pacific Ocean, and are clearly intermediate between the more common spirally coiled Neritinæ and the genus *Septaria* (= *Navicella* Lamarck), which is confined to the same regions. On the other hand, the expanded American species of *Neritina*, e. g. *latissima* Brod. and *intermedia* Sowerby, retain the distinct

dextral coil of the spire and their shells are asymmetrical, in general form somewhat like *Haliotis*. The same is the case with *N. oweniana* Gray, from the W. Coast of Africa, Fernando Po, and Cape Palmas; and thus it appears that the Neritinæ of rivers running into the Indian and Pacific Oceans (but not of American rivers on the Pacific slopes) have given rise to the limpet-like fluviatile genus *Septaria*, whilst those of the Atlantic shores have followed a different line of evolution and have in no case given rise to *Septaria* forms.

The genus *Septaria* Férussac is commonly referred to in zoological works as *Navicella* Lamarck, but Férussac's name has the priority and, according to all rules of zoological nomenclature, ought to be adopted. It appears to be a characteristically fresh-water genus, living on the roots of Nipa palms and other trees on the banks of rivers in India, Mauritius, Bourbon, N. Australia, and the Pacific Islands. The *Septariæ* of the Mascarene Islands and Madagascar affect the vicinity of waterfalls, and are found adhering to stones out of the water but constantly wetted by spray. Due allowance being made for the secondary symmetry which they have acquired, the internal anatomy of individuals of this genus closely resembles that of *Nerita* and the tropical Neritinæ. Little or nothing is recorded of the breeding-habits and development of *Septaria*, but some specimens of *S. bougainvillei* Récluz, a Fijian species in my possession, have egg-cases, resembling those of *Neritina fluviatilis*, attached to the shell, each case containing a number of veliger larvæ.

No more than a passing mention can be made here of the Titiscaniidæ, of which *Titiscania* Bergh is the sole genus. It is a slug-like marine form, probably widely distributed in the Indo-Pacific seas, but hitherto recorded only from the Philippines and Mauritius. It is a highly specialized member of the Neritacea, with something of the form and habits of a Nudibranch. The shell is lost, but the ctenidium and mantle-cavity, though reduced, remain. Bergh (2) has given an account of the anatomy of this remarkable genus, from which it is evident that it is rightly placed among the Neritacea, and probably near to *Neritopsis*, because of the absence of the median plate in the radula. There are, however, many imperfections in Bergh's account of the anatomy. Believing that the supra-intestinal nerve was absent in *Nerita*, he failed to find it in *Titiscania*, and we are left in doubt as to whether it is really present in the latter genus or not. For similar reasons doubt must be thrown on his description of the heart with a single auricle, and his account of the generative organs is so wanting in precision and detail that one can only gather from it that the accessory glands and ducts are complicated, and may very possibly resemble those of *Nerita*.

The remaining families of the Neritacea, the Helicinidæ, Proserpinidæ, and Hydrocenidæ, are, as is well known, terrestrial pulmonate forms, with the habits of snails. Their distribution coincides on the whole closely with that of the tropical *Neritæ*

and *Neritinæ*. The Helicinidæ occur chiefly in islands in the Indo-Pacific region, and in the Antilles, reaching their maximum in the last-named locality. As has been already remarked, they are only found fossil in later Tertiary deposits, with the exception of the remarkable *Dawsoniella*, which occurs in the Carboniferous of Illinois, and is apparently related to *Trachydomia*, a subgenus of *Naticopsis*, from the same formation. The present distribution and the geological history of these Pulmonate Neritacea suggest problems which will be dealt with in the second part of this paper. With the exception of *Dawsoniella*, they are unquestionably descended from Neritid or Neritinid ancestors, and it is difficult to account for their dispersal in islands so widely separated from one another without making assumptions which differ widely from accepted doctrines of animal evolution.

It was my original intention to undertake a monographic account of the anatomy of the Neritacea, but as the work proceeded it became evident that, owing to the difficulty of obtaining suitable material, and the great number of species which must necessarily be subjected to microscopical examination before completeness could be attained, this would be a task of many years' duration. The results already attained seem of sufficient importance to merit publication, and may induce zoologists travelling or living in tropical regions to give attention to a group deserving more attention than it has received. I therefore purposely omit a detailed account of certain organs, such as the buccal bulb, the radula, and the histology of the alimentary tract, the mantle, &c. My chief attention has been directed to the nervous system, the kidney, the pericardial cavity and its connection with the rest of the cœlom, and the generative organs.

The difference between the aquatic Neritidæ and the terrestrial pulmonate Helicinidæ is so considerable that they must be dealt with in separate sections of this memoir, and in each case, in order to avoid a confusion of my own observations with a criticism of the work of other authors, I will preface my statements with a short account of the literature of the subject.

Family Neritidæ.

The first important contributions to the anatomy of *Nerita* are those of Quoy and Gaimard (**35** & **36**), whose figures and descriptions of the nervous system and alimentary tract leave much to be desired, and it is not necessary to enter into an examination of their errors and omissions. But they made some observations on the generative organs which, though far from complete, have not been followed up, and have scarcely been noticed by any subsequent author except Bergh. It will be best to quote their description in full:—"Dans le sexe femelle est un groupe d'organes qui mérite quelque attention. On y voit l'extrémité du rectum, puis un corps pyriforme très-allongé entouré en partie d'une sorte de glande striée en travers, qui s'ouvre vers le bas.

Cet organe est creux et contient dans sa cavité, accollés les uns aux autres, plusieurs corps en massue allongée, finissant en filaments. Ils sont résistants, comme fibreux, et paraissent grenus à la loupe. Nous ne pouvons deviner l'usage de ce petit appareil, qui remplit sans doute quelques fonctions relatives à la génération, puisqu'on ne le trouve que chez les femelles. Plus en dehors est l'utérus, composé d'une poche pyriforme et d'un renflement qui lui est accollé, lequel contenait une grande quantité d'œufs, ronds blancs et crétacés. L'oviducte, gros long et tortueux, fait communiquer cet organe avec l'ovaire, placé au bord droit du foie." Though this description and the figure accompanying it are inexact, it is evident that the "corps pyriforme" is the spermatophore-sac, the "corps en massue allongée" are the spermatophores, the "glande striée en travers" is the ootype, with its glandular walls, the "uterus," as described and figured by these authors, has no separate existence, but the "renflement qui lui est accollé" is the crystal-sac, which does, in fact, open into the distal end of the ootype. It also seems probable that MM. Quoy and Gaimard mistook the spherical crystalline concretions in the crystal-sac for ova.

Of the male, Quoy and Gaimard give a very insufficient account of the accessory generative organs, but observed the excessively long coiled region of the sperm-duct to which I have given the name of epididymis.

In an earlier memoir Quoy and Gaimard (**35**) gave a superficial account of the structure of *Nerita*, which only merits attention because it contains two figures showing the modification of the cephalic integument at the base and to the inside of the right tentacle of the male, which has been referred to, but seldom correctly figured or described, by subsequent authors as a "cephalic penis." In the figures referred to this structure is represented in the correct position, but simply as a conical eminence, without any detail.

From the time of Quoy and Gaimard there is no work dealing with the anatomy of *Nerita* till that of Bouvier in 1886. Von Jhering (**22**), in his well-known work on the nervous system of mollusca, abruptly removes the whole of the Neritacea from their position alongside of the other Rhipidoglossa and places them in a class Orthoneura, which has long since been broken up, its contents being restored to their proper places by subsequent and more exact observers. But his investigations were confined to the nervous system of *Neritina fluviatilis*, and had he carefully studied the anatomy of some of the larger species of *Nerita* or of a *Septaria* he would probably have paused before promulgating the opinions set forth in his lengthy memoir.

Bouvier (**8**), in a preliminary note published in 1886, gave a short account of the principal external features of the anatomy of *Nerita* and some details of the nervous system, but the reader should turn for a more complete account to his great work (**9**) on the nervous system of prosobranchiate Gastropods. As he

himself subsequently corrected his errors about the nervous system, it is not necessary to dwell on what is now a matter of history. Failing to recognize the extremely fine supra-intestinal nerve in any of the Neritidæ he dissected, he wrote with characteristic emphasis, "Il n'y a pas de commissure viscerale croisée," and classed the Neritacea as "Rhipidoglosses orthoneuroïdes." Following de Lacaze-Duthiers, he identified the swollen origin of the subintestinal nerve with its sheath of ganglion-cells as the subintestinal ganglion, but, curiously enough, did not observe the large ganglion on the visceral commissure, afterwards discovered and called the subintestinal by Béla Haller (**20**) and Boutan (**6**). But his description of the nervous system is much in advance of anything that preceded it. He was the first to discover the course of the subintestinal nerve and of the left pallio-branchial nerve. He discovered and described correctly the labial commissure, characteristic of the more primitive prosobranchs. This commissure, as he says, is "très facile à préparer," and it is curious that Béla Haller, who succeeded in the much more difficult task of tracing the supra-intestinal nerve, should have emphatically denied the existence of this very obvious labial commissure. There is a further point of difference between these two authors, in which Bouvier appears to me to be correct. Béla Haller describes no less than fourteen transverse commissures behind the anterior commissure of the pedal nerve cords, whereas Bouvier found, as I find, nothing more than fine nerves passing from the inner sides of the cords to the muscles of the foot. In Bouvier's brief account of some of the more important anatomical features of *Nerita peloronta* there is a curious misprint, which has created some confusion among some subsequent authors. On p. 47 he writes: "Au fond de la cavité branchiale, à *droite*, se trouve la branchie bipectinée, libre en avant, en arrière rattachée au manteau à droite et à gauche par un expansion de la lame médiane, de sorte que le fond de la cavité branchiale est divisé en deux étages superposés. A *gauche* de la branchie se trouve le rein; il s'ouvre dans la cavité branchiale par un orifice en boutonnière situé dans la paroi antérieure du nucléus." The words italicised ought to be transposed: the ctenidium, of course, is on the left side of the mantle-cavity, and the kidney is to the right of the ctenidium. Bouvier further describes the so-called cephalic penis "toujours assez réduit dans les Nérites," and gives a figure of a remarkable development of this organ in *Neritina cariosa*. Though his description and figure are not very clear on this point, Bouvier appears to have determined the true position of the osphradium in *Nerita*, but as he did not examine the structure of this organ and did not recognize the ganglia connected with it, his determination is rather of the nature of a conjecture than of proof.

The next contribution to the anatomy of *Nerita* is that of Rémy Perrier (**34**), whose researches were confined to the kidneys and associated organs in *Nerita peloronta*, *Neritina*

oweni, and *Septaria* (*Navicella*) *janelli*. The position and general anatomy of the kidney of *Neritina fluviatilis* had been previously described by Landsberg (**24**); and Perrier adds some details relating to the trabecular structure of the excretory portion of the kidney and the reno-pericardial canal. He did not, however, fully elucidate the relations of the glandular and non-glandular parts of the kidney, and described the latter as a closed sac intervening between the kidney and the pericardium. This error was afterwards corrected by Lenssen. The most important part of Perrier's work, in so far as it relates to the Neritidæ, is his account of the heart. He discovered and gave an accurate figure of the left auricle and showed that, contrary to Landsberg's statements, the ventricle is in fact traversed by the rectum.

Bergh (**2**) in 1890, as an addendum to his paper on *Titiscania*, gives an account of the anatomy of *Nerita peloronta* and *Neritella* (*Neritina*) *pulligera*. This is the first attempt, since Quoy and Gaimard, to give a complete account of the anatomy of *Nerita*, but it is unfortunately very incomplete and contains some serious errors and omissions. For example, Bergh denies the existence of a second auricle, and lays considerable stress on its absence. He describes the eyes as open, whereas they are in fact closed. His description of the nervous system, correct enough as far as it goes, is no advance on the original description of Bouvier. He gives a more or less detailed and tolerably correct account of the buccal bulb, odontophore and radula, and notes the presence of salivary glands, but mistakes an œsophageal dilatation for the stomach, and describes the true stomach as enlargements of the hepatic ducts. The position of pericardium and kidney are correctly described without adding anything to previous knowledge of the subject; but the reno-pericardial duct was not recognized. All of Bergh's specimens appear to have been females, and he makes an attempt to describe the complicated accessory generative ducts and glands, but, as he says, "bei den vorliegenden Materiale konnten die ganz unklaren Verhältnisse dieser Theile nicht genauer eruirt werden." He recognized, however, the spermatophore-sac, and gives a good outline figure of a spermatophore of *N. pulligera*.

In 1892 two short papers by Boutan (**6**) and Bouvier (**10**), the atter published very shortly after the former, established the existence of a supra-intestinal nerve in *Nerita* and *Septaria*, thus restoring the Neritacea to their proper place among the Streptoneurous Rhipidoglossa. Shortly afterwards Boutan (**7**) published a further account of the nervous system of *Nerita polita* and *Septaria* (*Navicella*) *porcellana*, in which the course of the supra-intestinal nerve is correctly figured, but he failed to recognize the supra-intestinal ganglion which Bouvier had signalized in the previous year. Boutan appears to have been in error as to the position of the osphradium, which he says "s'étend le long du septum branchial qui réunit la branchie au plancher de la cavité et est à peine distinct à l'œil nu." The osphradium, as I shall

show, is in fact in front of the suspensory membrane of the ctenidium, close behind the thickened margin of the left side of the mantle and in front of the anterior end of the left columellar muscle. Close below the osphradium is a complex of ill-defined ganglionic enlargements, and as Boutan failed to find the true osphradium he missed the ganglia lying beneath it. In this same paper Boutan argues, erroneously as I now think, that the so-called subintestinal ganglion of Bouvier is not a member of the group of visceral ganglia and gives figures of the pleuro-pedal ganglia of *Nerita* and *Septaria* correcting the older figures of the latter author.

In the following year Béla Haller (**20**), in the course of his studies on docoglossate and rhipidoglossate Prosobranchs, gave a tolerably full account, not only of the nervous system, but also of the alimentary tract, kidneys, and genital organs of *Nerita ornata*. This work contains a curious mixture of acute and accurate observations and incomprehensible errors and omissions. His elaborate figure of the nervous system is in some respects the best that has been published, but in other respects is most misleading. As has already been mentioned, he flatly denies the existence of a labial commissure, which is not only certainly present, but much easier to dissect than in any other Rhipidoglossate. I can positively assert that the numerous pedal commissures figured by Béla Haller are not present: Bouvier was perfectly correct on this point. In a simple dissection, one may easily make mistakes in attempting to trace delicate nerves through the mass of muscle in which they are embedded, but a study of microscopical sections leaves no room for error. A careful examination of a series of sections of several species fails to reveal any trace of transversal commissures posterior to the main pedal commissure. B. Haller discovered the supra-intestinal nerve, independently it seems of Boutan and Bouvier, and gives a fairly correct figure of the crossed visceral commissure. Like Boutan he identifies the elongated ganglion on the right of the crossed visceral commissure as the subintestinal, but he did not see the stout nerve given off from it, almost immediately swelling up to form the genital ganglion lying on the oviduct or sperm-duct. In respect of the supra-intestinal and branchial or osphradial ganglia, Haller gives a complicated figure which, as far as I am able to reconstruct these ganglia from serial sections, may be correct, but after many attempts I have been unable by simple dissection to verify his account. These ganglia are covered by the thickened and folded epithelium of the osphradium, which in all the species at my disposal is too opaque to allow the ganglia to be seen by transparency.

Haller's description of the alimentary tract is much more accurate than that of his predecessors. He gives a good account of the position and general relations of the stomach, œsophagus, and course of the intestine, but his observations on the buccal bulb, salivary glands, &c. seem to me defective. He describes

and figures a posterior diverticulum of the buccal bulb which I have failed to discover either in sections or by dissection, and his drawing of the salivary glands is incorrect in detail. In describing the heart he has, curiously enough, fallen into the same error as some of his predecessors, since he categorically denies the presence of a rudimentary right auricle: "da von einem rechten Vorhof nicht einmal ein Rudiment mehr erhalten ist."

After criticizing Perrier's account Béla Haller gives a somewhat detailed description and a figure of the kidney of *Nerita ornata*, but neither description nor figure is correct. According to him the kidney is an acinous gland, not differentiated into anterior and posterior lobes differing in histological structure. The ducts of the acini unite and open by large apertures directly into the bladder (Urinkammer). The reno-pericardial canal opens into the bladder and is dilated into a large sac which runs back posteriorly between the pericardium and the ureter, and is identified with the cavity described by Perrier as lying between pericardium and kidneys and incapable of being injected from the general body-cavity. I shall prove, in due course, that the glandular part of the kidney is not acinous, that there is a histological differentiation between the anterior and posterior moieties, that there are not several ducts leading from the glandular part to the ureter, and that the reno-pericardial canal opens not into the bladder but into the glandular portion.

As for Haller's description of the male and female generative organs, I need only say that his work is scarcely an advance on that of Claparède, and he failed to discover the remarkable complexity of these organs, which, indeed, could hardly have been discovered without careful and laborious reconstruction of sections.

It could not be guessed from the title "Die systematische Stellung der Solenogastren und die Phylogenie der Mollusken" that Thiele's (**39**) memoir, published in 1902, contains a number of new and acute observations on the morphology of the Neritacea. Interpolated as they are in a lengthy discussion of the phylogenetic history of the Gastropoda, Thiele's results are somewhat difficult to summarize, and it is to be regretted that he did not see fit to embody them in a separate memoir. He studied sections of *Nerita pica*, *Septaria parva* and *suborbicularis*, *Scutellina cinnamomea*, and *Helicina japonica*. It should be noticed in the first place that he places *Scutellina* without comment among the Neritidæ. *Scutellina* was classified by Fischer (**15**) among the Docoglossa, by Pilsbry and Tryon (**40**) near the Haliotidæ, and I have been unable to discover what author detected their relationship to the Neritidæ. It is clear, however, from Thiele's account of the female generative organs that it belongs to the last-named family. After touching on various points of the anatomy of the Neritidæ, such as the ctenidium, which he compares with that of the Acmæidæ rather than the Trochidæ; the subpallial sense-organ, which he describes and figures correctly but is

inclined to identify with the subpallial sensory tracts of Patellidæ, &c., rather than with a true osphradium; the left columellar muscle, which he considers to be derived from the subdivision of the primitive right muscle; the salivary glands, in respect of which he corrects the statements of Haller and Amaudrut, Thiele proceeds to give a more detailed account of the accessory genital organs. Though his diagrams are too schematic, his drawings of sections too few in number, and his description too condensed to convey a clear impression to anyone unfamiliar with these complex structures, his account of the female organs of *Nerita pica* and *Septaria parva* is very exact, both as regards the general anatomy and the histology. I shall have occasion to refer frequently to it in the descriptive part of this paper. It need only be mentioned here that he does not appear to have found spermatophores in the spermatophore-sac, and therefore is obscure as to the function of this organ. Though he found and has figured the peculiar crystalline concretions in the crystal-sac, he names this structure the uterus—for insufficient reasons, as it appears to me. He did not discover the oviduco-cœlomic funnel, and does not mention the presence of the third duct, which I have called the ductus enigmaticus in *Septaria parva*. It is of course possible that it is not present in this species. The description of the female organs of *Scutellina cinnamomea* leaves no doubt that this form is a member of the Neritidæ. The description of the male organs of *Helicina japonica* will be dealt with in the second part of this paper, and I can supplement it by an account of the female organs of *Alcadia*. Thiele regards the "receptaculum seminis," *i. e.* the spermatophore-sac, as the representative of the right kidney in female Neritidæ, and though I do not agree with this conclusion it is not far from the truth.

Further on Thiele gives a description of the kidney in *Nerita pica* and in *Septaria*, and here also makes more accurate observations than any of his predecessors. He also notices the extension of the pericardial cavity to the right side of the animal in *Septaria*, and makes a just comparison between the conditions obtaining in this animal and the Cephalopoda. In conclusion, Thiele suggests that the Neritidæ may have been derived from the Trochidæ, but points out features in which they show a resemblance to the Docoglossa. The latter, however, as he says, are more probably analogies than homologies, as the radula and the structure of the generative organs preclude any idea of close relationship between these groups.

The genus *Neritina*, owing to the abundance of the common *N. fluviatilis* in European rivers, has been more often and more thoroughly studied than the genus *Nerita*. It is not necessary to do more than refer to the works of Moquin-Tandon (**28**), Claparède (**12**), and Landsberg (**24**), or to the paper on the development of *Neritina* by Blochmann (**4**), because the results obtained by these authors have already been discussed and entirely superseded by the admirable papers of Lenssen (**25** & **26**). In the first

of these two papers Lenssen deals with the digestive and genital systems, giving a detailed account of the bucco-pharyngeal cavity, the odontophore, the œsophagus with its glandular appendages, and the stomach. He and Gilson (18) are the only authors besides Thiele who have published an accurate account of this system of organs in the Neritacea. Gilson and Lenssen discovered the remarkable fact that in *Neritina*, a dicœcious Gastropod, the female ducts are diaulic, whereas the male ducts are monaulic; and the latter author gives a thorough and accurate description of the very complex arrangements of both male and female organs. I have only to say that I have carefully verified Lenssen's statements and find nothing to correct and very little to add to them as regards the species examined, *Neritina fluviatilis*, but I find considerable and important differences in some of the tropical Neritinæ.

In his second paper Lenssen deals with the nervous, circulatory, respiratory, and excretory systems of *Neritina fluviatilis*. Here he has not been in some respects as accurate as in his first paper. For instance, in the description of the nervous system (p. 297) he confuses the labial with the buccal commissure. It is clear both from his text and figure that the commissure that he discovered is the buccal commissure, but he calls it the labial.

It is practically impossible to dissect out the true labial commissure in so small an animal as *N. fluviatilis*, and it is exceedingly difficult to trace it in sections; but I have satisfied myself that it exists. In other respects Lenssen's account and figure of the nerve-centres appear to be correct, and I can confirm his statement that there are no transverse commissures behind the single large commissure uniting the anterior ends of the pedal cords.

As regards the visceral and pallial nerves Lenssen makes a considerable advance on his predecessors and he accepts Bouvier's identification of the subintestinal ganglion. He discovered, apparently without being aware that Boutan and Béla Haller had anticipated him in this matter, the ganglion on the subintestinal nerve at the point where the latter turns rather sharply from right to left to course close below the surface on the dorsal side of the pedicle attaching the anterior part of the body to the visceral mass. His account of the relations of this ganglion and of the nerves given off from it is for the most part very exact, but he does not appear to have observed that the genital nerve (*loc. cit.* pl. i. fig. 1, *ns.*) almost immediately enlarges to form a ganglion of considerable size, closely attached to the oviduct (or sperm-duct). He further describes a structure which he hesitates to identify as the rudiment of the right ctenidium. "A cet endroit," he says, "il existe un organe creux, l'homologue, peut-être des mamelons découverts chez les patelles et d'autres prosobranches. Cet organe renferme un grand nombre de globules sanguins et semble, par conséquent, dépendre soit de l'appareil circulatoire, soit de l'appareil respiratoire. Il fait saillie dans la

cavité branchiale et s'ouvre à sa base dans le sinus sanguin que nous venons de signaler." Further on (p. 312) he discusses the homology of this organ and suggests that it may represent the right ctenidium or the right osphradium, but gives no decided opinion on this point. A description and discussion of the significance of this organ will be found on p. 864.

Though he made, as he tells us, a careful search for it, Lenssen failed to discover the supra-intestinal nerve; but being cautious he does not venture to affirm that it does not exist. Nor am I ready to deny its existence, but after searching most carefully through several series of sections I am unable to discover a trace of it; and it is very possible that this nerve, extremely small in *Nerita* and the tropical species of *Neritina*, has actually disappeared in *N. fluviatilis*. In the descriptive part of this paper I shall have something to add to Lenssen's account of the left branchial ganglion and the osphradium. It is not necessary for me to refer at length to Lenssen's account of the circulatory, respiratory, and excretory systems. Though somewhat short, his descriptions of these systems are accurate so far as they go, and he is the first author to give a true and intelligible account of the kidney and reno-pericardial duct.

I make no separate reference to the literature bearing on the anatomy of *Septaria* (*Navicella*). This genus has not been studied in detail by any author, but Bouvier, Boutan, and others have described the nervous system in the works already quoted. As my interest in the Neritacea dates from some dissections of *Septaria* which I made for the purposes of my class, and as the secondary symmetry acquired by this genus makes it a very favourable object for describing and figuring the somewhat complex relations of the cœlom and genital ducts in the Neritacea, I will begin the account of my own work with a description of its anatomy.

Genus Septaria Férussac.

The species of this genus available for my researches were *S. borbonica* Bory, *S. depressa* Lesson, both forming part of the collections of the Oxford Museum, and *S. bougainvillei* Récluz, from the British Museum. The number of specimens at my disposal was small, and I unfortunately dissected the only two specimens of *Septaria borbonica* that I possessed before I had made myself thoroughly familiar with the problems of Neritacean anatomy. A specimen of *S. depressa* was cut in horizontal and one of *S. bougainvillei* in transverse sections. Both these specimens proved to be females. There are some minor points of difference in the anatomy of the two species which will be referred to in due course.

A dorsal view of *S. borbonica* is given in fig. 1*. The roof

* The figure-numbers 1–69 in this Memoir refer to the figures on Plates XLVI.–LXVI., which are described on pp. 885–837. There is only one text-figure (text-fig. 172, p. 853).

of the mantle-cavity has been cut through and largely removed to show the principal organs of the pallial complex. The head is relatively large; the tentacles short and swollen at their bases; the eyes, as in all Neritacea, borne on prominences at the outer sides of the bases of the tentacles. Owing to the abortion of the visceral spire the animal has acquired a secondary symmetry, which does not, however, extend to the more important systems of organs. The right and left columellar muscles, *cm.l* and *cm.r*, are subequal in size and symmetrically disposed right and left of the body. The visceral spire is reduced to a triangular mass at the posterior end of the body. To the right side of the mass is the ovary, *ov.*; the left side is occupied by the stomach covered over by the liver.

The mouth, situated on the ventral side of the head, is at the end of a very short snout, which can be scarcely retractile. The foot is large and oval, occupying nearly the whole of the ventral surface behind the snout: it is surrounded by a rudimentary epipodial ridge. The operculum is wedged in between the viscera and the upper surface of the foot, extending as far forward as the posterior end of the buccal bulb. It is functionless, at any rate as regards the closing of the aperture of the shell, but it seems to give support to the muscles of the foot, and retains a rudiment of the apophyses characteristic of the opercula of the Neritidæ.

On the dorsal side, after the removal of the roof of the mantle-cavity, the single bipectinate ctenidium, the post-torsional left, is seen lying obliquely across the mantle-cavity, its base attached to the left side and its free end pointing forward and to the right. As in most ctenidiate Neritacea, the proximal moiety of the ctenidum is attached by a suspensory membrane to the right and left walls of the mantle-cavity, in consequence of which arrangement the posterior half of the cavity is divided into an upper and a lower chamber.

The heart, enclosed in a spacious pericardial cavity, lies on the left side, just behind and below the posterior end of the left columellar muscle. It cannot be seen in a dorsal view, but its position is indicated by *pc*. The rectum, after traversing the ventricle, crosses obliquely from right to left just in front of the visceral mass, is partly embraced by the complex mass of accessory genital glands and ducts, *g.d*, and opens by the anus near the anterior end of the right columellar muscle. The kidney, *k*, lies between the rectum and the basal half of the ctenidium: it opens by a slit-shaped pore into the lower chamber of the mantle-cavity close to the right side of the base of the ctenidium, but the opening cannot be seen in the drawing. It is perhaps necessary to state here that the kidney is the post-torsional left, as has been fully recognized by recent authors on Molluscan anatomy. It is therefore the homologue, not of the large functional kidney of other Aspidobranchia, but of the so-called papillary sac of Trochidæ and Haliotidæ, and of the rudimentary left kidney of the Docoglossa.

The Alimentary Tract.

Fig. 2 is an illustration exhibiting the macroscopic characters of the buccal bulb, œsophagus, stomach, and intestine. It would be possible to write at considerable length on the structure and histology of these various regions, but I purposely refrain from doing so, although my preparations have enabled me to study them with considerable accuracy. Allowance being made for small and unimportant differences in proportion and detail, the structure of the alimentary tract of *Septaria* is so closely similar to that of *Neritina fluviatilis* as described by Lenssen (25), that it is superfluous to give a description which would be little more than a repetition of his accurate observations. I need only call attention to one or two minor points. I find that in *Septaria*, as in *N. fluviatilis*, there are seven buccal cartilages, three pairs and one median and azygos. The smallest pair, discovered for the first time by Lenssen, does not strictly belong to the odontophore, but lies in the antero-inferior walls of the buccal bulb and serves as supports for a pair of pads, covered by a horny cuticle, against which the right and left halves of the anterior end of the radula work. In *Septaria* there is a small pair of glandular sacs, one on each side, opening into the lateral extensions of the subradular diverticulum of the buccal cavity. These have been noted by Thiele in *Nerita pica*, but are not recorded by Lenssen in *Neritina fluviatilis*. The œsophagus in *Septaria* passes to the left on leaving the buccal bulb and shows clear traces of the larval torsion so carefully described by Amaudrut (1). Just before its junction with the stomach it expands considerably and receives three large ducts from the liver. The œsophagus may be said to join the stomach tangentially; hence its aperture is prolonged backwards as a wide groove, bounded by thickened epithelial lips, which, while they differ slightly in detail, have the same relations as are described by Lenssen in *Neritina fluviatilis*. The stomach of *Septaria* consists, as is the case in all the Neritidæ I have examined, of a dilated œsophageal and a narrower pyloric moiety. In the former there is a large and prominent epithelial ridge, described by Lenssen as the "crête stomacale," conspicuous for its triangular appearance in section. Its extremely long columnar epithelial cells are always covered by a thick apparently cuticular product, which in appearance and composition seems to be similar to the cuticular lining continuous with the crystalline style found in so many Molluscs. In *Septaria* there is a small digitiform diverticulum of the œsophageal moiety of the stomach, situated between the lower end of the "crête stomacale" and the upper border of the œsophageal groove. This diverticulum, which is probably homologous with the spiral diverticulum of the stomach of *Haliotis*, appears to be absent in *Neritina fluviatilis*. The intestine and rectum do not call for any special mention. The histology of the different regions varies, and the variations have been sufficiently described by

Lenssen. The disposition of the coils of the intestine and their relations to the stomach, œsophagus, and radula-sac are indicated in fig. 2, as is also the position of the heart and the fact that the ventricle laps completely round the rectum. The radula-sac is large and usually of considerable length, but varies considerably in different specimens. When long it is involved in the coils of the intestine and its posterior part always passes ventrad of the œsophagus but dorsad of the stomach.

The Nervous System.

The main features of the nervous system have already been described by Bouvier (**9** & **10**) and Boutan (**7**). The latter author, correcting and amplifying the earlier account of Bouvier, describes a supra-intestinal nerve completing the streptoneurous condition of the visceral nerve, and gives an amended figure of Bouvier's drawing of the pleuro-pedal nerve-centres. In my earlier dissections I failed to identify the supra-intestinal nerve, but have been able to follow its course more or less completely in my serial sections, and am able to verify Boutan's statements as far as they go. In one particular I can add to them. Boutan traced the supra-intestinal nerve from its origin from the right pleural ganglion along the right side of the body, whence it turns over the gut towards the left side and courses, as he says, "dans la cavité branchiale, au niveau du tiers inférieur de la branchie." It is hardly correct to say that the nerve passes into the branchial cavity. After a considerable amount of trouble I have been able to trace the nerve as far as the osphradium, the precise character and position of the latter organ having been overlooked by Boutan. The supra-intestinal nerve on arriving at the left side of the body passes obliquely forward in the connective tissue underlying the integument on the dorsal side of the left columellar muscle. Near the anterior end of this muscle the nerve passes upward, and without any ganglionic enlargement on its course, it joins the elongated ganglion underlying the osphradium in the left anterior corner of the mantle-cavity. The osphradial ganglion is also supplied, as is the case in *Nerita* and *Neritina*, by the symmetrical left branchio-pallial nerve, emanating from the left pleural ganglion. This large nerve traverses the columellar muscle and passes almost direct to the osphradium, where it enlarges to form the above-mentioned ganglion. From the ganglion a branch passes along the anterior border of the left suspensory fold of the ctenidium and may be traced without difficulty nearly to the tip of the latter organ. Another branch passes backwards, nearly parallel to the columellar muscle. I have not been able to trace this nerve in its entirety, but have no doubt that it is the continuation of the supra-intestinal nerve, and joins the visceral ganglion in the vicinity of the uropore, thus completing the visceral loop. If this is the case the streptoneury is complete, as it is in *Nerita* and the larger tropical species of *Neritina*.

In order to avoid repetition of details I will pass briefly over the rest of the nervous system of *Septaria*. In all essential features it resembles the nervous systems of *Nerita* and the tropical Neritinæ, which I shall describe in greater detail in the subsequent part of this paper. I need only say here, because Béla Haller has thrown doubt upon these points in his description of the nervous system of *Nerita ornata*, that there is a well-defined labial commissure in *Septaria*, and that I can find no trace of transverse commissures, posterior to the main anterior commissure, between the pedal cords in this genus.

The position and structure of the subpallial sense-organ or osphradium in the Neritidæ has been correctly described by Bernard (3) and Thiele, but the latter author throws doubt on its homology with the true osphradium of other Mollusca, and other authors give doubtful or incorrect descriptions of it. In *Septaria* this sense-organ is easily distinguished in transverse sections as a prominent ridge of epithelium running forward from the anterior end of the left suspensory fold of the ctenidium along the roof of the mantle-cavity and ending only a short distance behind the thickened anterior edge of the mantle. It lies almost in the angle formed by the union of the mantle with the left columellar muscle, and its position at the inhalant side of the mantle-opening is consistent with the function usually attributed to an osphradium, that of a sense-organ for testing the quality of the water before it passes over the ctenidium. The cells covering this ridge are higher, their nuclei are more closely crowded together and stain more deeply than those of the adjacent mantle epithelium. Under a high power of the microscope the epithelial ridge can be resolved into three parallel strips. The two outer strips (*a–b* and *b–c* in fig. 17) consist solely of columnar epithelial cells with granular cytoplasm and rather large nuclei. The free ends of these cells bear cilia which in the groove shown on the lower side of fig. 17 are longer than elsewhere. The central strip (*b–b* in fig. 17) is largely composed of the same elements, but its character of a sensory epithelium is well shown by the presence of a number of attenuated sense-cells, interspersed between the larger columnar cells. The nuclei of the sense-cells are smaller and more elongated than those of the columnar cells; their cell-bodies stain deeply in carmine, and in many cases it can be seen that their inner ends are prolonged into fine fibrils which traverse the thin layer of muscle-fibres and connective tissue underlying the osphradium and pass into the osphradial ganglion. The size and position of this ganglion at the place where it is joined by the large branchio-pallial nerve are shown in fig. 17.

The respiratory and circulatory systems have been worked out in some detail by Lenssen in *Neritina fluviatilis*, and their arrangement is similar in *Septaria*, but allusion must be made to one or two points in which Lenssen's account is defective.

The ctenidium in *Septaria* is an elongated triangular organ, its free pointed extremity directed forward and to the right; its

base attached to the body-wall on the left side. It consists of a flattened axial plate containing blood-spaces, with numerous gill-lamellæ running transversely across its dorsal and ventral surfaces. The ctenidium is therefore typically bipectinate. Unlike that of *N. fluviatilis* its posterior half is attached, on the left side to the mantle close to its union with the columellar muscle, on the right side to the lower surface of the kidney, by a membranous suspensory fold. Thus the posterior part of the mantle-cavity is divided into an upper and a lower chamber. A large blood-vessel runs along each edge of the axial plate, and in the upper and lower wall of each vessel there is a stout band of longitudinal muscle-fibres, which must serve as retractors of the gill and also assist in the circulation of blood through the gill-lamellæ. On the right-hand is the afferent and on the left the efferent branchial venous sinus. The two do not communicate with one another at the apex of the gill but only by the lacunar passages in the gill-lamellæ and the axial plate. The general course of circulation in the gill is as follows:—Blood is brought to the gills from the large venous sinus underlying the kidney by the afferent branchial sinus. This sinus does not communicate, as may be seen by inspection of fig. 20, with the cavities of the axial plate, except at very rare intervals, but it is in free communication above and below with the cavities of the gill-lamellæ, and its blood passes into these latter and circulates through them. The cavities of the gill-lamellæ and also that of the axial plate are broken up by numerous trabeculæ or partitions passing from wall to wall and are bounded by a thin layer of connective tissue containing a few muscular fibres. The margin of each gill-lamella is somewhat swollen and contains a cavity or vessel which, as far as I can ascertain, is continuous from one end of the lamella to the other, and also is in free communication with the irregular spaces below. At the opposite side of the gill these marginal vessels open into the efferent branchial sinus. The innermost cavities of the gill-lamellæ open from place to place into the system of lacunæ in the axial plate, and these, uniting to form a large lacuna near the left edge of the axial plate, also open at frequent intervals by large apertures into the efferent branchial sinus. It is obvious that the blood on entering the gill-lamellæ from the afferent sinus may either take a direct course to the efferent sinus by way of the marginal vessels of the lamellæ, or may traverse the lacunæ in the adaxial part of the lamellæ, pass into the system of lacunæ in the axial plate, and thence be discharged into the efferent sinus.

The distribution of ciliated epithelium on the faces of the gill-lamellæ is of some interest. Each gill-lamella is an extremely delicate plate of semilunar form, its straight inner margin attached to the axial plate, its curved margin free and, as described above, somewhat thickened. When one attempts to separate the lamellæ by the aid of needles one recognizes that their central portions adhere very closely together, whereas their

lateral portions are readily parted from one another. When a single lamella is separated out, stained and examined under the microscope, it has the appearance shown in fig. 23, the dark central tract with diverging horns being the expression of numerous deeply stained and closely packed nuclei in this region. In short, the epithelium covering the lamellæ is not uniform. The following arrangement can be determined in section :—The lateral tracts of each face of each gill-lamella are clothed by a cubical epithelium containing isolated or grouped gland-cells of oval shape with clear contents. The epithelial cells of these tracts (if they are ciliated at all, which I am inclined to doubt) bear exceedingly short and fine cilia. The thickened margin of the lamella always bears three or four "frontal" cells at its extreme edge; these cells, as in the gills of Lamellibranchia, carry a tuft of short rather stiff cilia. External to them are a few cells devoid of cilia, and at the extreme ends of the lamellæ large gland-cells alternate with the epithelial cells of this region. Sections through the dark median band with its two horns show that this is a tract of more columnar cells, closely packed together, with deeply staining nuclei, each carrying a tuft of very long cilia which interlock with those of the adjacent lamella and are the cause of the adherence noted above.

There are no supporting rods or skeletal bars, such as those described by M. F. Woodward in *Pleurotomaria*, but, as shown in fig. 21, the connective tissue underlying the epithelial cells is thickened near the attachment of each gill-lamella to the axial plate. There is some resemblance between the arrangement of the lateral cilia in *Septaria* and other Neritidæ and in *Pleurotomaria*, and by parity of reasoning the ciliated tracts of the former genus must differ from those of Lamellibranchia in the same manner that Woodward has shown them to differ in the case of the latter genus. It is interesting to note the structural analogies of gastropod and lamellibranch gills. In the case of the Neritidæ the ciliated tracts fulfil the same functions as the ciliated discs of the Filibranchia. But their arrangement is different. The cell-mechanism is the same, but it cannot be doubted that it has been independently evolved in the two groups, affording a good instance of the evolution of similar but not identical structure in similar organs subject to similar conditions.

Lenssen, describing the gills of *Neritina fluviatilis*, has given an incorrect account of the epithelium. He figures an almost uniform covering of ciliated cells, and among them a few gland-cells. I have found the same arrangement in *N. fluviatilis* as in *Septaria*, and Lenssen would appear either to have altogether overlooked the ciliated tracts, or to have confused in a single drawing and description the ciliated cells of the one tract and the glandular cells of the other. It is curiously difficult to obtain good preparations of the gills of *N. fluviatilis*, and if my attention had not been called to the subject by the much more obvious

arrangement of the cells in *Septaria*, I should have overlooked it. As it is I have identified a similar gill-structure in *Nerita plicata*, *N. variegata*, *Neritina gagates*, and *N. longispinosa*. The description given above is therefore characteristic for the ctenidium of the Neritidæ, and will not be repeated in dealing with other species.

The branchial nerve, derived from the ganglion underlying the osphradium, runs through the suspensory membrane and along the outside of the efferent branchial vessel in the free moiety of the gill. This nerve has been noted by nearly all previous authors, but only Bernard has described a nerve running down the other side of the gill, in connection with the afferent branchial vessel. Such a nerve, embedded in the dorsal longitudinal muscle, is present in *Septaria* and is shown in fig. 20, *br.n.* As far as I can determine from my sections it communicates with the nerve on the efferent side by a slender connection at the tip of the gill. It is thickest in the posterior part of the course, and passes into the right suspensory membrane in the direction of the visceral ganglion; but try as I might, I could not trace it through the suspensory membrane to the ganglion.

The Circulatory System.

Lenssen's account of the heart and blood-vessels in *N. fluviatilis* is in all essential features applicable to *Septaria*. I need lay stress on a few points only. The ventricle in *Septaria* is thick and muscular and is completely wrapped round the rectum. I wish to emphasize this point, because some authors have stated that the ventricle is only partially attached to the rectum in Neritidæ, and have contrasted this with the conditions found in Haliotidæ and Trochidæ. Practically the supposed difference does not exist.

The blood from the efferent venous sinus passes directly into the left auricle, and at the point where the efferent sinus joins the auricle a large pallial sinus, bringing back blood from the numerous lacunæ of the roof of the mantle-cavity, opens into it. This pallial sinus has been recorded by Lenssen in *N. fluviatilis*, but I think he underrates its importance. In *Septaria*, at any rate, its diameter is nearly equal to that of the efferent branchial sinus, and it is connected with so extensive a system of blood-lacunæ in the mantle that there can be no doubt that the latter is a very important auxiliary organ of respiration. The blood, therefore, which reaches the ventricle by way of the left auricle has been oxygenated either during its passage through the ctenidium or through the mantle, but none of the pallial blood passes through the ctenidium. The importance of the pallial circulation in *Septaria* is further indicated by the relatively considerable size of the right auricle. This organ, the relations of which may easily be traced in sections or by simple dissection, passes from that part of the ventricle lying posterior to the rectum, across the pericardial cavity, and is attached to the left body-wall just at the level of the

left posterior corner of the foot. Here it receives blood from two venous sinuses: the one bringing back blood from the left posterior region of the body-wall, the other from a considerable system of lacunæ in the posterior part of the foot. The former of these two sinuses runs in close connection with the posterior lobe of the kidney, and it would appear that we have here an arrangement whereby oxygenated blood from the mantle is also enabled to get rid of its waste nitrogenous products before it is returned to the heart. This is the reverse to what occurs in the case of the blood passed through the ctenidium, which is first purified of its nitrogenous waste matter during its passage through the sinuses of the anterior lobes of the kidney and is afterwards carried to the ctenidium by the afferent branchial sinus. The right auricle, like the left, is covered by the glandular tissue of the pericardial gland. As *Septaria* has undergone a considerable amount of detorsion, it is evident that the position of the right auricle, and its connection with the left and posterior part of the body-wall and foot, is a secondary phenomenon, due to its movement from right to left, in the direction of the hands of a clock, during the process of detorsion. In fact, one can only use the term "right" in a morphological sense, to indicate that this auricle would be on the right if the typical gastropod torsion had been maintained. In the genera *Nerita* and *Neritina*, as will be seen, the rudimentary auricle is more distinctly on the right side, but even in these forms posterior to the ventricle. The size of the right auricle varies much in the Neritidæ. It is always present, but in some of the typically marine forms such as *Nerita peloronta* it is so small and unimportant that it might easily be overlooked, and indeed its existence has been denied by Béla Haller. In the tropical Neritinæ, many of which are semi-aquatic in habit, spending no inconsiderable part of their lives on the roots of trees above low-water mark, or even above high-water mark of neap-tides, the right auricle is larger and receives the same blood-supply as in *Septaria*. The last-named genus is one that, according to all accounts, has progressed further than any other Neritid in the direction of a terrestrial life, living as it often does on stones in the vicinity of waterfalls where it is only wetted by spray. One might expect, therefore, that it would exhibit a more marked tendency to the replacement of a branchial by a pallial respiration, and such has been shown to be the case. It is of special interest to observe the connection between a more highly developed pallial respiration and the increased size and importance of the right auricle, for, as I shall show in the second part of this memoir dealing with the Helicinidæ, there is every reason to believe that in the last-mentioned family, in which the ctenidium is lost and the respiration is entirely pallial (or, as it is called, pulmonary), the single auricle that persists is the right and not, as has generally been supposed, the left.

The courses of the main efferent or arterial vessels proceeding from the ventricle, and the venous sinuses in the foot and visceral

cavities, are so similar in *Septaria* to those described by Lenssen in *Neritina fluviatilis*, that it is not necessary to enter into any further description of them.

The Hæmocœle and Cœlom.

The cavities in which lie the buccal bulb, the œsophagus, radula-sac, and the coils of the intestine are, as is usually the case in Molluscs, a vast blood-space or hæmocœle. In most Neritidæ and in the Helicinidæ this space is largely filled up by a parenchymatous tissue, which from its structure and position appears to be metabolic in function and probably serves for the storage of reserve material. Where present it is aggregated along the courses of the chief arterial vessels, and a certain amount of it is to be found surrounding the anterior aorta in *Septaria*. This metabolic tissue, however, is never abundant in *Septaria*, and I postpone a description of it to the section dealing with the *Neritæ* and *Neritinæ*. In *Septaria*, and indeed in all Neritidæ, the large hæmocœlic cavity does not extend as a wide space into the visceral mass of the spire. In this region nearly the whole of the space contained within the body-walls is occupied by the ovary, the stomach, and the mass of the liver lying above and to the right side of the stomach. It is only on the left side that some distinct posterior prolongations of the hæmocœle are visible surrounding the intestine, the left and lower sides of the stomach, and the radula-sac. The great anterior hæmocœlic space surrounding the pharyngeal bulb and the greater part of the coils of the intestine is often referred to by writers on molluscan anatomy as the anterior body-cavity, and allusion is sometimes made to a sort of diaphragm or partition shutting off this anterior cavity from the visceral cavity behind. In fact, there is no definite diaphragm or dissepiment, and the appearance of one is due to a somewhat complex union of muscular membranes connected with the kidneys and genital ducts, but particularly to a large venous sinus with muscular walls passing from the right towards the base of the ctenidium. In this space lies the elongated visceral ganglion.

Theoretically the visceral hæmocœle is to be regarded as a continuous space, the hinder part of which is filled up by the stomach and liver. This can be understood by reference to fig. 41, illustrating a horizontal section through the ventral part of the body of *Neritina gagates*.

With regard to the cœlom, Lenssen observes with much truth that in *Neritina fluviatilis* it is the most extensive space in the whole body. "En avant," he says, "elle (la cavité péricardique) se prolonge jusqu'à la base de la branchie, et de là, s'élargissant de plus en plus en arrière, elle s'étend sur toute la largeur du corps et divise l'animal en deux portions bien nettes. Sa paroi supérieure se confond avec la base du rein et se prolonge sous l'utérus; elle sépare le rein du foie. Sa partie inférieure, chargée de pigment, enveloppe le massif formé par les circonvolutions de

l'intestin et du sac radulaire dans la région antérieure du corps et se prolonge en arrière jusqu'à l'origine du rein." This description is tolerably exact, but the ramifications of the cœlomic cavity are extremely difficult to make out in *Neritina*, and a much clearer picture of the extent and relations of the cœlom can be obtained from the more symmetrical *Septaria*. In this genus, as may be seen in fig. 4, the cœlom is, relatively to the size of the body, a vast space extending from right to left across the entire width of the visceral mass.

Two divisions can be recognised, the pericardial and the gonadial cœlom. The former lies to the left; it is traversed by the bend of the rectum, contains the heart, and communicates by the reno-pericardial duct with the kidney. The gonadial division of the cœlom lies on the right, and may be described in general terms as intervening between the liver and ovary and the dorsal body-wall in the region of the visceral mass (fig. 4, *g.co.*). Near the anterior border of the visceral mass it forms a spacious cavity extending downward on the right side of the body to the level of the floor of the visceral hæmocœle, and here it enters into remarkable relations with the oviduct. As shown in figs. 3, 4, and 5, the oviduct, which pursues a nearly straight course forward from the ovary to the accessory genital apparatus, crosses the gonadial cœlom, and at this point opens into it by a distinct but short and narrow oviduco-cœlomic duct, the details of which are indicated in fig. 5. The duct is lined by a cubical epithelium bearing fine cilia, and this, near its opening into the gonadial division of the cœlom, is replaced by an epithelium containing closely crowded, deeply stained nuclei and bearing longer cilia. The similarity between this oviduco-cœlomic funnel and duct and the reno-pericardial canal of the left side is obvious, and affords evidence of the former existence of a right kidney, into which, as in other Rhipidoglossa, the ova were discharged to find their way to the exterior by the right uropore. The full significance of these relations will be dealt with further on: it need only be said here that the existence of an oviduco-cœlomic funnel, opening into a special division of the cœlom, is not parallelled in any other adult Gastropod, except the allied genera *Nerita* and *Neritina*.

The pericardial division of the cœlom is of large size: it extends forward to the base of the ctenidium and is continued for some little distance along the left edge of the latter, parallel to the efferent branchial vessel, as a narrow diverticulum. Posteriorly the pericardial cavity extends along the left side of the stomach nearly to the pointed extremity of the visceral mass. The gonadial division of the cœlom is a more irregular cavity. In the anterior part of the visceral mass, immediately behind the accessory genital organs, it is of considerable vertical depth, reaching from roof to floor of the visceral sac in front of the liver and ovary. A little further back it extends over the liver and ovary and to the right of the latter as far as the floor of the

visceral sac, but on the left it appears in sections only as a narrow cleft reaching as far as the rectum. Posteriorly the gonadial cœlom gradually becomes smaller and smaller, as the liver and ovary project further into it, and eventually it is reduced to a comparatively narrow space between the rectum above and the radula-sac and liver below. In the region of and behind the ventricle the two divisions of the cœlom communicate freely with one another by a large slit-like passage which, as shown in fig. 4, *c.ap.*, lies dorsad of the stomach. The pericardial floor leading to it is deeply pigmented.

The Excretory System.

The kidney in *Septaria* is more easily studied than in any other member of the Neritidæ, and my investigations confirm the correctness of Lenssen's somewhat brief account of this organ in *Neritina fluviatilis*. The kidney of *Septaria* is an elongated organ lying transversely across the posterior third of the body, closely attached to the left and anterior side of the rectum where the latter passes across from the pericardium to join the complex mass formed by the accessory genital organs (fig. 1, *K.*). The left and posterior end of the kidney lies close below the dorsal body-wall (fig. 4, *K.*); its right and anterior moiety passes into the dorsal wall of the mantle-cavity. Throughout the whole of its extent it is in close relation to the pericardial division of the cœlom. The kidney may be described in general terms as a tubular organ bent upon itself in such a way that its two ends are anterior and open respectively into the mantle by the uropore and into the pericardial division of the cœlom by the reno-pericardial duct. Only the dorsal limb of the tube is glandular, its cavity being traversed by a number of deep infoldings of its lateral walls, which in turn give off secondary folds (fig. 18, *K.*). There is no question of an acinous structure such as has been described in *Nerita ornata* by Béla Haller (20). As Lenssen describes for *Neritina fluviatilis*, the partitions which cross the cavity of the glandular part of the kidney of *Septaria*, though they may sometimes appear in sections to cross from wall to wall, are really infoldings of the lateral walls terminating in free edges within the cavity of the kidney. The whole of the glandular part is surrounded by a system of blood-sinuses (fig. 19, *b.si.*), connected with smaller sinuses running in the partitions, and a distinct sinus or vessel may often be recognized along the free edges of the latter. The epithelium clothing the walls and partitions of the glandular part of the kidney is non-ciliated, but is not of uniform character throughout. In the right and anterior moiety of the kidney the cells are dilated by the presence of a large transparent vacuole at their free ends; the nucleus lies in the basal part of the cell, stains faintly, and is surrounded by a small amount of cytoplasm. In the left and posterior moiety of the kidney the cells are more prismatic, are less vacuolated, their nuclei stain more deeply and are situated

nearer to the middle of the cell-body. The different appearance of these two regions of the glandular part of the kidney, as seen under a low power of the microscope, is represented in fig. 18. It may be thought that this apparent distinction is due to a difference in the secretory activity of the cells, but I have found it to be so constant a feature in the different species of *Nerita* and *Neritina* that I have studied that I think there must be some functional differentiation between the two regions. The glandular part of the kidney opens posteriorly into the non-glandular part or bladder, the latter being a large flattened sac of irregular form running forward between the glandular part and the pericardium. It is this sac which Perrier described as a closed cavity interposed between the kidney and the pericardium, and Béla Haller was scarcely more correct in identifying it as the reno-pericardial duct. Anteriorly the bladder expands towards the right (fig. 19) to form a diverticulum lying below and behind the venous sinus in which the ascending portion of the sub-intestinal nerve is contained. The tough membranous walls of this diverticulum of the kidney-sac and of the venous sinus form together with the anterior wall of the gonadial cœlom the so-called diaphragm referred to on p. 834. The left anterior corner of the bladder passing below the glandular part turns upward as a narrow passage lying between the latter and the base of the ctenidium, and twisting over to the right opens into the lower chamber of the mantle-cavity by the uropore below and to the left of the afferent branchial sinus. By far the greater part of the bladder is lined by a non-ciliated flat epithelium, but in the duct leading to the uropore this is replaced by a ciliated epithelium composed of very long attenuated and transparent ciliated cells. The reno-pericardial canal, as is the case in all Neritidæ, is very large. It opens, as shown in fig. 18, *rp.c.*, into the anterior end of the glandular part of the kidney; thence running to the left and posteriorly, it becomes closely attached to the wall of the duct of the bladder in the vicinity of the uropore, and twisting downwards and inwards it describes an S-shaped curve and opens by a wide ciliated aperture into the base of the anterior diverticulum of the pericardial cavity referred to above as extending forward alongside the efferent branchial sinus. The epithelial cells of the reno-pericardial duct are very large and each bears a tuft of long stiff cilia. Lenssen has given a figure of this characteristic epithelium in *Neritina fluviatilis*, and describes it as a good example of a discontinuous epithelium. His figure is a good representation of the appearance usually seen in sections, but from what I have seen in some well-preserved specimens I think that the apparent discontinuity is due to contraction produced by reagents.

It follows from the above description that the kidney of *Septaria* (the kidney of other members of the Neritidæ is similar) is not a simple glandular sac, but is composed of a glandular and non-glandular part the relations of which are very similar to those observed in the lamellibranchiate kidney. In *Septaria bougainvillei*

there is no communication between the anterior ends of the glandular and non-glandular parts. The exception is shown in fig. 19, representing part of a horizontal section through *Septaria depressa*. In this the terminal portion of the non-glandular part is seen to communicate with the glandular part by a small but perfectly distinct orifice in the vicinity of the renal aperture of the reno-pericardial duct. I can find no trace of such an orifice in *S. bougainvillei*, but it occurs in several other Neritidæ. It is not an accidental rent in the wall, the epithelium passing in unbroken continuity round the lips of the orifice.

It is now so generally understood that the kidney of the Neritidæ is the post-torsional left, that it is not necessary for me to insist upon the further evidence in support of this opinion derivable from the facts just mentioned. But it is perhaps necessary to allude to the question as Fleure (17) in a comparatively recent paper has attempted to prove that the single kidney of the Neritidæ and Pectinibranchia is the left post-torsional and corresponds with the large functional left kidney of most Rhipidoglossa. Unfortunately for his argument his paper is followed by that of Miss Drummond (13), in which the fact previously insisted on by von Erlanger (14) is placed beyond all doubt, namely that the existing kidney of *Paludina* (and presumably of other Pectinibranchs) is the post-torsional left. The rudiment of the post-torsional right kidney becomes converted into the genital duct in the course of embryonic development It is clear, from the presence of the oviduco-cœlomic funnel, that the same thing has happened in the Neritidæ.

The Generative Organs.

Gilson (18) was the first to give an intelligible account of the female generative organs of *Neritina fluviatilis*, and their structure was subsequently worked out in great detail by his pupil Lenssen. More lately Thiele has described these organs in several species of Neritidæ, including *Septaria* (*Navicella*) *parva* and *suborbicularis*. A further description would therefore seem superfluous, were it not that *Septaria* differs in some not unimportant particulars from *Neritina*, and Thiele's account of the former genus is little more than a brief note, omitting histological detail, and, moreover defective in at least one very important particular. Moreover, as a result of a comparison of Lenssen's and Thiele's work with my own and of an attempt to homologize the different cavities, ducts, and glands in the different forms that I have examined, I have come to conclusions somewhat different from those of the two authors named, and have to suggest a new nomenclature for the different parts. Gilson and Lenssen have shown that the female ducts of *Neritina fluviatilis* are diaulic; Thiele has made the same statement for *Nerita* and *Septaria*. A reference to the diagram (fig. 3) will show that the female ducts of *Septaria* are triaulic There is the large *ovipository aperture* (*Ov.ap.*), through which the

eggs enclosed in their egg-shells are extruded; the copulatory or *vaginal aperture* (*vag.ap.*), through which the sperm of the male is received; and a third minute aperture (*ap.de.*) situated further back, whose function I cannot determine: I shall refer to it as the aperture of the *ductus enigmaticus*. This third aperture is not present in *Neritina fluviatilis* nor in the marine species of *Nerita*, but is present in all the fresh- or brackish-water tropical species hitherto classed as *Neritina*. To begin with a description of the diagram, fig. 3. The ovipository aperture leads into a vast pouch with thick glandular walls. This has been called the "uterus" by Gilson and Lenssen, the "shell-gland" by Thiele. As there is no doubt that the egg-shell is formed from the secretion of the glands opening into this cavity the latter name is appropriate, but it will avoid confusion if I borrow a name from an analogous structure in the Platyhelmia and call it the "ootype."

A flattened saccular diverticulum (*cry.s.*), lying on the right side of the terminal part of the ootype, opens into the latter not far from the ovipository aperture. In the species I examined it is of small size and does not contain concretions or foreign bodies, but it is clearly homologous with the "poche à cristaux" of Lenssen, and I shall refer to it as the *crystal-sac*. In *Nerita* and *Neritina* it is relatively large and filled with spherical crystalline bodies. Thiele calls this sac the uterus, but the name is inappropriate, for there is no evidence whatever that the ova are passed into it.

The relations of the ootype may be studied in the series of transverse sections (figs. 6–12). Anteriorly it lies above and partly embraces the rectum. In this region its walls are very thick and glandular, its cavity large, crescentic, and simple. Further back it lies to the right of and apart from the rectum, and its cavity becomes more complicated in form. The whole organ is spirally twisted, so that the concavity of the crescent, which was at first directed downwards, is in fig. 9 directed upwards. In fig. 10 the left-hand corner of the cavity is seen to be prolonged into a diverticulum, which in fig. 11 turns sharply to the right and runs back parallel to its former course. From this, which may be described as the terminal part or fundus of the ootype, two passages are given off in different directions. The one, which I shall call the *egg-duct*, leads to the oviduct and through this to the ovary. The other establishes a connection with the vagina and ductus enigmaticus and serves for the admission of spermatozoa to the fundus of the ootype.

The egg-duct (*eg.d.* in figs. 10–13) is characterized by the different forms of glandular tissue constituting its walls. Its opening into the cavity of the ootype is embraced by a glandular thickening distinguishable from the fact that its cell-contents do not stain in any of the ordinary dyes: this I call the *clear gland*. As shown in figs. 11, 12, 13, it is largely situated in a tongue-shaped projection of the right-hand wall of the fundus, which appears to function as a valve guarding the passage from the

fundus into the egg-duct. The dorsal side of the egg-duct is capped by a considerable glandular mass (*m.gl.*), whose contents stain deeply in hæmatoxylin: it may therefore be identified as a *mucous gland*. Beyond this is a narrow ring of glandular tissue whose cell-contents stain bright rose-red colour in eosin and carmine dyes: for this reason I shall refer to it as the rose-coloured gland (figs. 12–14, *rc.gl.*). Beyond the rose-coloured gland the egg-duct dilates to form a distinct chamber with thick glandular walls. This chamber corresponds to the "première ampoule" of Lenssen; I shall call it the *thalamus* (figs. 14, 15, 16, *th.*). It occupies the right-hand posterior corner of the genital complex, and the gland surrounding it may from its position and staining-properties be identified as the *vitelline gland*. The *oviduct*, a narrow tube lined by a columnar ciliated epithelium, emerges from the lower left-hand corner of the thalamus, runs towards the left, is thrown into a few convolutions, then turns sharply backward and downward and enters the connective-tissue layer forming the floor of the large right extension of the gonadial cœlom. In its passage below this cœlomic space it gives off a short branch to the right, which immediately opens into the cœlom by a ciliated oviduco-cœlomic funnel (figs. 3 & 4, *od.c.f.*). Beyond the oviduco-cœlomic funnel the oviduct branches repeatedly; the branches subdivide and end in a number of claviform acini lined by a germinal epithelium and containing ova in all stages of development. The ovary, thus constituted, is a fairly extensive organ lying to the right of the liver and spreading for some distance over its dorsal surface.

The second passage leading out of the fundus of the ootype is a narrow thin-walled tube which passes to the right and immediately dilates to form a sac of considerable size lying between the posterior end of the ootype and the rectum. As this sac always contains free spermatozoa in greater or less abundance, it may be called the *sperm-sac*. Its walls are thin, usually much folded, and lined by a simple cubical ciliated epithelium without any trace of glandular structure. In longitudinal section it is seen to be U-shaped.

From the bend of the U a short duct is given off posteriorly. It has thick muscular walls, and ends in a thick-walled dilatation, filled with spermatozoa. This is the *receptaculum seminis* (=spermatheca of Gilson). The limbs of the U are prolonged forward as two narrow ducts, which acquire thick muscular walls and open separately into the mantle-cavity. The outer or right-hand duct corresponds to the "connecting duct" of Gilson and Lenssen. I shall call it the *vaginal canal*. The inner or left-hand duct is not represented in *Nerita* or in *Neritina fluviatilis*, and as its function is obscure I have named it the *ductus enigmaticus*. The two ducts run forward close to one another and to the rectum. The ductus enigmaticus is relatively short and straight, and eventually opens into the mantle-cavity by a minute pore situated on the ventral side of the genital complex and some

distance posterior to the anal and ovipository apertures (fig. 6, *ap.de.*). The vaginal canal runs parallel to the ductus enigmaticus as far as the opening of the latter, and then bends abruptly backward. Its lumen becomes very narrow, and its muscular wall relatively thick; after a short course backward it opens by a minute pore into a sac (*sp.s.*), which corresponds to the copulatory vesicle of Gilson and Lenssen, the receptaculum seminis of Thiele. As may be seen in the diagram, it is the dilated posterior end of the *vagina* (*vag.*), and is of small size in *Septaria borbonica* and *bougainvillei*. But in the tropical *Neritinæ*, in *Nerita*, and, according to Thiele, in *Septaria parra* it is relatively of enormous size and invariably contains a number of spermatophores of complex structure. Hence I shall call it the *spermatophore-sac*, although I have not found a trace of spermatophores in any of the specimens of *Septaria* that I have examined. The lumen of the spermatophore-sac gradually diminishes anteriorly and passes without sensible alteration of structure into the *vagina*, which opens into the mantle-cavity by the vaginal aperture situated on a prominent papilla some little way in front of the anus.

Gilson has given a clear account of the process of fertilization in *Neritina fluviatilis*. Owing to the small size of the spermatophore-sac it must be somewhat different in *Septaria borbonica* and *bougainvillei*. The spermatozoa must be deposited by the male in the vagina and must travel by way of the vaginal canal to the receptaculum seminis, where they are disposed, just as Gilson describes, in a very regular manner, all heads turned towards the centre of the vesicle and all tails directed outwards. At the time of impregnation the spermatozoa must be passed, by contraction of the muscular walls of the receptaculum and its duct, into the fundus of the ootype and thence into the egg-duct, where the ova are fertilized. The function of the ductus enigmaticus can only be guessed at. It may serve to admit water into the cavity of the sperm-sac, or contrariwise may serve for the expulsion of fluids accumulating in the sperm-sac.

Histology of the Genital Ducts.

From what precedes it will have been gathered that there are five different kinds of glands on the course of the ootype and egg-duct, viz., the vitelline gland, the rose-coloured gland, the mucous gland, the clear gland, and the ootype or shell-gland. Similar glands occur in the same positions in all the Neritidæ I have studied, including *Neritina fluviatilis*. The histology of the shell-gland of the last-named species has been correctly described by Lenssen, but he gives a very summary, and, in the case of the vitelline gland at least, a somewhat incorrect account of the remainder. The important thing is that all the glands are of the same fundamental structural plan, and only differ from one another in the proportions and staining-properties of the cells and the secretions produced by them. It may therefore be inferred that

the community of structure is due to community of origin ; and if it can be shown that there is a transition between the secretory epithelia of the glands and the epithelia of other regions, there is a presumption in favour of the view that the glands are derived from those other epithelia. A transition can be demonstrated between the epithelium of the mantle-cavity and that of the shell-gland. The epithelium lining the mantle-cavity differs considerably in different parts, but in the neighbourhood of the ovipository aperture it consists of fairly high columnar ciliated cells, among which are numerous gland-cells with granular contents, which in *Septaria* stain bright green in picro-indigo-carmine. This epithelium is continued over the lip of the ovipository aperture into the terminal part of the lumen of the ootype, and, extending further down on the right side than elsewhere, forms the lining of the crystal-sac. Elsewhere it quickly undergoes a change : the gland-cells disappear, and the ciliated cells increase in length, become attenuated, and are separated by considerable intercellular spaces (fig. 24). This simple ciliated epithelium is continued downward for some little distance, and only gradually becomes complicated by the appearance at first of a few club-shaped gland-cells lying between the ciliated cells. The gland-cells contain large granules, highly eosinophilous, or staining bright green in picro-indigo-carmine. The gland-cells soon become more abundant, and some of them, while retaining their connection with the surface, tend to take up a deeper position. Their swollen inner ends, containing the nucleus and most of the cytoplasm, pass through the thin layer of muscle-fibres underlying the ciliated epithelium and embed themselves in the surrounding connective tissue, their distal ends being drawn out into fine tubes which pass between the ciliated cells and open into the cavity of the ootype. In good preparations the walls of these tubes are quite distinct, and each tube contains a single row of eosinophilous granules, but swells out in the intercellular space between the ciliated cells, so that it appears to terminate in a claviform vesicle distended with granules (fig. 25). A little further down the gland-cells increase in number and form groups, and these groups passing into the surrounding connective tissue form at first shorter, but in the greater part of the ootype relatively long, club-shaped masses surrounding its cavity. The club-shaped masses have the appearance of and have been described as crypts, but are not to be regarded as such, for what appears to be the cavity of the crypt is occupied by the tubes, and there is no lumen into which the secretion is discharged, but each cell has its own duct opening on the surface. This may readily be seen in transverse sections of the so-called crypts in good preparations. It would be more correct to describe each group of cells as a bunch, the deeper cells having very long hollow stalks and the more superficial cells shorter stalks; all the stalks pass between the ciliated epithelial cells, become slightly swollen, and open on the surface. The manner in which this somewhat

elaborate arrangement is derived from a comparatively simple mixed ciliated and glandular epithelium is very well shown in the terminal chamber of the male ducts of *Nerita* (fig. 52). Precisely the same fundamental structure is found in all the glands on the course of the female ducts. In the ootype gland the cell-bodies are coarsely granular and stain deeply in hæmatoxylin, the granules of secretum are highly eosinophilous, and the ciliated cells are moderately long. In the "clear gland" the cytoplasm of the gland-cells is scarcely granular, is not stained appreciably by any of the ordinary dyes, the "stalks" or ducts of the cells are relatively large, their contents clear and unstained by reagents. The ciliated cells are somewhat widely spaced, and conspicuous because they are not hidden by granules in the secreting ducts (fig. 27).

In the "mucous gland" the bunches of glandular cells are large; the gland-cells are dark and granular and their cytoplasm stains deeply with hæmatoxylin and picro-indigo-carmine. The secretory granules are not so large as in the uterine gland, are of unequal size, and as they are not eosinphilous, but stain blue with picro-indigo-carmine and deeply with hæmatoxylin, they are probably mucinogenous. The ciliated epithelial cells between which the unicellular ducts run are very much elongated.

In the "rose-coloured gland" the bunches of gland-cells are rather small; their cytoplasm stains rose-pink with picro-indigo-carmine, carmine, or eosin; they are not granular, and their ducts contain a non-granular coagulum which is highly eosinophilous. The ciliated cells are short.

In the "vitelline gland" (fig. 28) the cell-bunches are of moderate size; the gland-cells have a reticular cytoplasm staining faintly with picro-indigo-carmine or hæmatoxylin; the secretory granules are small, of equal size, and faintly stained by the reagents mentioned; the ciliated cells forming the boundary epithelium are clearly defined and of moderate length.

It is evident that, although it is not possible to attribute precise functions to the different glands, they are to be regarded morphologically as differentiations of a tract of mixed glandular and ciliated epithelium, the histological characters of which are such that it is in the highest degree probable that it has been formed as an invagination of the mantle-epithelium—that is to say, of the ectoderm. The histology of the vagina, vaginal duct, sperm-sac, and ductus enigmaticus is quite different. These organs are non-glandular, and are all lined by a very similar ciliated cubical epithelium, which at first sight does seem to be very similar to the epithelium of the oviduct, and different from that of the mantle-cavity. But a careful examination with high powers of the microscope shows that they are different. In the oviduct the cytoplasm of the cells is differentiated to form a distinct refractive external border, the cilia are longer and stouter, the nuclei are more elongated and stain more intensely than is the case in the bursa copulatrix and the ducts leading from it. Moreover, when the vaginal duct is

traced to its aperture, which in *Septaria* lies some way in front of the anal and ovipository apertures, the epithelium of the duct is seen to pass without any distinction of histological character into the epithelium of the adjacent part of the mantle-cavity, which latter is not in this place glandular, as it is close by the anal and uterine orifices, but is a simple ciliated columnar epithelium resembling the epithelium of the terminal portion of the vaginal duct in the minutest particulars. The ductus enigmaticus opens into a region of the mantle in which the epithelium has been greatly modified by the abundant development of long beaker-shaped mucous cells, and in this case the transition from the epithelium of the duct to that of the mantle is abrupt (fig. 6). From a consideration of these facts I am inclined to the opinion that the whole of the sperm-sac and its two ducts is also formed as an invagination of the mantle-epithelium, and that therefore the whole of the accessory organs contained in the genital complex, with the exception of a short length of the oviduct, are ectodermal structures secondarily attached to the oviduct; and in this I differ from Thiele (39), who regards the whole of the vagina and sperm-sac (which he calls the receptaculum seminis) as the representative of the right kidney of the Neritidæ. There can be no doubt that the distal portion of the oviduct represents a part, probably the terminal part or duct, of the right kidney. The existence of the oviduco-cœlomic funnel is sufficient evidence of this homology. But in my opinion the limit between kidney derivative and ectodermal derivative is indicated in *Septaria* by the opening of the oviduct into the thalamus. Here there is an abrupt change in the histological character of the epithelium, and a reference to figs. 3, 13, & 16 shows that the thalamus and the egg-duct intervene between the oviduct and the sperm-sac. I have given strong reasons for believing that all the glands of the thalamus and egg-duct are derived from the ectoderm; and if I am right this circumstance militates against Thiele's view that the spermatophore-sac represents the right kidney, for it can hardly be maintained that ectodermal structures have pushed their way into the primitive kidney and divided it into two widely separated parts, one opening to the exterior, the other communicating with the cœlom by a ciliated funnel.

I am unable to give a description of the male organs of *Septaria*, as all the specimens that I have examined by means of sections were females.

From an inspection of fig. 4 it might be inferred that the extensive tubular gland lying in the dorsal body-wall to the right of the rectum, and therefore occupying on the right side of the body a position similar to that occupied by the kidney on the left, is a representative of the glandular part of the right kidney. Such an inference, however, cannot be sustained. The histological characters of the gland in question are indistinguishable from those of the hypobranchial mucous gland of other Rhipidoglossa (e. g. *Fissurella*). The anterior lobe of the gland lies immediately

behind the genital complex—some of its tubules are seen in figs. 15 & 16,—and its duct issues from the anterior lobe, passes ventrad of the receptaculum seminis, and opens into the right-hand side of the mantle-cavity just below and to the right of the oviduco-cœlomic funnel. It will be observed that the gland in *Septaria* lies on the right side of the rectum, and cannot therefore be the exact homologue of the hypobranchial gland of the Trochidæ, which lies to the left of the rectum, between the latter and the left ctenidium to which it is related. It must rather be regarded as the homologue of the right hypobranchial gland of the dibranchiate Rhipidoglossa, and it seems probable that it represents the additional gland of the right side described by M. F. Woodward (41) in *Pleurotomaria*. The right hypobranchial (or additional hypobranchial) gland should be related to the right ctenidium, but this has apparently disappeared in the Neritidæ. I cannot find any vestige of it in *Septaria*, but in various species of *Nerita* and *Neritina* there is a small vascular organ projecting into the mantle-cavity close to the aperture of the hypobranchial mucous gland. This has been described in *Neritina fluviatilis* by Lenssen under the name of the "organe creux," and I shall show in the latter half of this paper that partly on account of its relation to the hyprobranchial gland there are good reasons for regarding it as the vestige of the right ctenidium.

Genera Nerita Adanson and Neritina Lamarck.

It would be possible to give a detailed account of numerous minute differences in the alimentary tract, minor branches of the nervous system, excretory organs, &c. in the various species of *Nerita* and *Neritina* that I have studied; but the enumeration of these details would be not only tedious but unprofitable. I have satisfied myself that in all essential features of the anatomy of the alimentary tract, nervous system, respiratory and circulatory systems, and excretory organs, the various species enumerated below are so similar to one another that they may be included in a single description. Moreover, their main anatomical features are so like those of *Septaria* that I may spare the reader the trouble of perusing a mass of detail which would differ only in unessential matters from what has already been described in the last-named genus. It is otherwise with the generative ducts, especially the female ducts. I shall have to point out that the specimens I have had the opportunity of examining fall into three groups, defined by the constitution of the genital ducts. The first group comprises the marine species unquestionably belonging to the genus *Nerita*, as defined in conchological works. The second group comprises the tropical species hitherto classed in the genus *Neritina* and the genus *Septaria*. The third group comprises the European *Neritina fluviatilis*, and to this must probably be added the various European species of *Neritina*; but I cannot say anything definitely on this subject, for I have not